

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PATRONS TEMPORELS ET SPATIAUX DE LA SÉVÉRITÉ DES ÉPIDÉMIES DE
LA TORDEUSE DES BOURGEONS DE L'ÉPINETTE EN RELATION AVEC LES
CONDITIONS BIOCLIMATIQUES DANS L'EST DU CANADA

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TEMPORAL AND SPATIAL PATTERNS IN THE SEVERITY OF SPRUCE
BUDWORM OUTBREAKS IN RELATION TO BIOCLIMATIC CONDITIONS IN
EASTERN CANADA

THESIS

PRESENTED IN PARTIAL FULLFILLMENT OF
A DOCTORATE IN BIOLOGY

BY

ELIZABETH MARIE CAMPBELL

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AVANT PROPOS

Cette thèse est soumise sous forme de cinq articles scientifiques. Pour chaque article, j'étais la personne principalement responsable pour le design d'expérimentation, la récolte et la compilation de données, les analyses statistiques, et la rédaction.

Le premier article est: « SPRUCE BUDWORM OUTBREAK DYNAMICS IN RELATION TO BIOCLIMATIC CONDITIONS OF BOREAL FORESTS IN NORTHWESTERN QUEBEC». Les autres auteurs étaient: Yves Bergeron and David MacLean. Cet article est en révision pour la Revue Canadienne de Recherche Forestière.

Le deuxième article est: « LOCAL STAND CHARACTERISTICS AND LANDSCAPE CONTEXT INFLUENCE THE SEVERITY OF SPRUCE BUDWORM OUTBREAKS IN BOREAL FOREST OF QUEBEC». Les autres auteurs étaient: Yves Bergeron et David MacLean. Cet article a été soumis à Ecological Applications.

Le troisième article est: « PATTERNS OF BUDWORM-CAUSED TREE DEATHS IN RELATION TO THE HARDWOOD CONTENT OF BOREAL FOREST LANDSCAPES». Les autres auteurs étaient: Yves Bergeron et David MacLean. Cet article est en révision pour Écoscience.

Le quatrième article est: «THE SEVERITY OF BUDWORM-CAUSED GROWTH REDUCTIONS IN BALSAM FIR/SPRUCE STANDS VARIES WITH THE HARDWOOD CONTENT OF SURROUNDING FOREST LANDSCAPES». Les autres auteurs étaient: David MacLean et Yves Bergeron. Cet article est sous presse à Forest Science.

Le cinquième et dernier article est: « INCORPORATING FOREST COMPOSITION EFFECTS ON DEFOLIATION INTO AN IMPLEMENTATION OF THE SPRUCE BUDWORM DECISION SUPPORT SYSTEM IN NORTHWESTERN QUEBEC ». Les autres auteurs étaient: Brendan Hemens, David MacLean, Yves Bergeron et Brian Harvey. Cet article est en préparation pour soumission à Forest Ecology and Management.

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RÉSUMÉ DE LA THÈSE

La dendrochronologie a été utilisée pour reconstruire les épidémies de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) dans 16 peuplements âgés de la forêt boréale du nord-ouest québécois. Épidémiques ont pu être déduites à partir de sept périodes prolongées de réduction de la croissance radiale chez *Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss: 1801-1813, 1823-1838, 1851-1867. L'estimation du temps de retour des épidémies était de 28-30 ans alors que la durée des épidémies était de 12-15 ans. La plus sévère épidémie observée depuis les 200 dernières années (1923-1934) a été associée aux températures élevées d'hiver, aux périodes humides prolongées et à l'abondance des *Abies balsamea* matures.

Vingt-huit peuplements dominés par des sapins baumiers ont été échantillonnés pour déterminer l'influence de la composition du paysage et des caractéristiques locales sur la sévérité des diminutions de croissance radiale causées par la dernière épidémie de TBE dans le nord-ouest du Québec (1971-1985). Les peuplements ont été classifiés en trois groupes distincts selon que les effets de l'épidémie sur la croissance y étaient légers, modérés ou sévères, avec des diminutions de croissance moyennes de 24 %, 44 % et 61% respectivement. Les épidémies furent plus sévères dans les peuplements où les hôtes ont été abondants et où le pourcentage des peuplements feuillus dans le paysage forestier a été plus faible. Les résultats de cette étude soulignent la nécessité de considérer le contexte spatial des peuplements pour évaluer leur vulnérabilité aux épidémies de TBE.

Dans ces peuplements sensibles aux épidémies, les patrons de mortalité des sapins suite à la dernière épidémie ont été étudiés en relation avec l'abondance de feuillus dans le paysage. Le pourcentage de sapins morts diminue significativement ($p < 0,05$) dans les peuplements à forte présence de feuillus à proximité. Alors que les gros sapins (> 20 cm) ont tous le même risque de mourir durant les épidémies, les plus petits sont dans 20% des cas moins susceptibles de mourir dans des peuplements entourés par des forêts feuillues. Les patrons temporels de mortalité des arbres varient également selon la présence de feuillus dans le paysage. Alors que la plupart des sapins ont été tués en 1984 dans les paysages contenant moins de 50% de feuillus, les peuplements entourés de plus de feuillus ont connu aussi de la mortalité mais sur une plus longue période. La variabilité des patrons de mortalité du sapin baumier qui a été observée est susceptible d'entraîner des trouées dans la forêt pouvant varier considérablement quant à leurs tailles et taux de formation, ceci pouvant avoir d'importantes implications dans les patrons de succession de la forêt suivant des épidémies de TBE. À ce sujet, quatre voies de succession potentielle sont proposées.

La variation dans la réduction de la croissance radiale des sapins lors de la dernière épidémie de TBE au Nouveau-Brunswick a été examinée en relation avec l'abondance des peuplements dominés par des feuillus dans la mosaïque forestière, l'historique des

pulvérisations d'insecticides ainsi que la topographie. L'abondance des peuplements feuillus dans la mosaïque forestière a expliqué 12% à 33% de la variation dans la diminution de la croissance entraînée par la TBE. Les différences dans la diminution de la croissance entre les peuplements étaient plus marquées au cours des années initiales de l'épidémie (1972-1980), particulièrement en 1976 alors que les réductions moyennes furent autour de 40% dans les peuplements composés de moins de 50% de feuillus et de 20% dans les peuplements composés de plus de 50% de feuillus. Les relations entre la variation dans la réduction de croissance entre les peuplements et la topographie ou l'historique des pulvérisations d'insecticides étaient moins constantes que celles avec l'abondance de feuillus dans la mosaïque forestière. Nos résultats laissent croire qu'augmenter l'abondance d'arbres feuillus dans le paysage forestier pourrait contribuer à réduire l'impact des épidémies de TBE sur les espèces résineuses commerciales.

Le Système d'Aide à la Décision concernant la tordeuse des bourgeons de l'épinette (SAD TBE) a été utilisé pour estimer les volumes de bois qui seraient perdus suite à une autre épidémie à la Forêt d'enseignement et de recherche du Lac Duparquet dans le nord-ouest du Québec. Les pertes de sapins et d'épinettes estimées ont varié de 0 à 92 000 m³ pour tous les scénarios d'épidémies modérées et de 80 000 à 148 000 m³ pour des scénarios d'épidémies sévères. Dans le premier cas, les variations dans les pertes estimées pourraient refléter des différences régionales dans la sévérité de la défoliation bien que cette tendance puisse être masquée par les types de données desquelles les modèles de prédiction ont été dérivés. Par ailleurs, les pertes prédites par les scénarios d'épidémies sévères ont différé sensiblement lorsque l'effet de la présence des feuillus dans les forêts sur les patrons de défoliation a été pris en considération. Les pertes estimées étaient de 17% moins importantes quand les modèles de défoliation tenaient compte de l'abondance des feuillus dans le paysage entourant le peuplement et de 46 % quand les modèles tenaient compte à la fois de l'abondance des feuillus dans les peuplements à l'étude de même que dans ceux les entourant.

Les résultats de la présente thèse ont permis d'enrichir les connaissances fondamentales concernant les épidémies de TBE, une perturbation naturelle et importante des forêts boréales et mixtes de l'est du Canada. Ces informations constituent une base de laquelle on pourrait mieux prédire les impacts des épidémies de TBE à venir et offrent des solutions de gestion pour minimiser leurs effets socio-économiques.

Mot-clés : *Tordeuse des bourgeons de l'épinette (Choristoneura fumiferana)*; *sapin baumier (Abies balsamea)*; *les impacts des épidémies d'insectes*; *dendrochronologie*; *biodiversité et le paysage forestier*; *le Système d'Aide à la Décision concernant la tordeuse des bourgeons de l'épinette*

1 INTRODUCTION GÉNÉRALE

Le maintien de la diversité biologique est considéré par plusieurs comme un moyen de préserver l'intégrité des écosystèmes forestiers, assurant ainsi un approvisionnement durable en biens et services directement reliés à la forêt (Hansen *et al.* 2004). On ajoute aussi qu'un maintien d'une composition et d'une structure forestière diversifiée devrait contribuer à l'atteinte de cet objectif. Bien qu'une proportion importante de la variabilité observée au niveau de la composition et de la structure des forêts soit reliée au climat et aux caractéristiques physiographiques (altitude, dépôt de surface, géomorphologie), les perturbations naturelles jouent aussi un rôle important. En effet, le type de perturbation, leur étendue, leur fréquence ainsi que leur sévérité lèguent une variété d'héritages écologiques déterminant en bonne partie la structure et la composition des forêts à de multiples échelles spatiales et temporelles (Pickett et White 1989; Frelich 2002). On percevait toutefois jusqu'au milieu des années 1980, et même au début des années 1990, les perturbations naturelles comme des agents destructeurs contre lesquels les gestionnaires devaient lutter. La suppression anthropique totale ou partielle de certaines perturbations naturelles ainsi que les aménagements forestiers tendent à générer une forêt plus homogène (Bergeron *et al.* 1998; Kuuluvainen 2002) et probablement moins résiliente aux perturbations futures (Drever *et al.* 2006). Ceci apparaît d'autant plus néfaste que les changements climatiques et les introductions d'espèces exotiques contribueront aussi à augmenter les risques de perturbations catastrophiques et autres (Taylor *et al.* 2006). Certains prédisent même que les pertes de biens et services rendus par les écosystèmes forestiers en résultant auront d'importants impacts socio-économiques (Hansen *et al.* 2004).

Les épidémies de tordeuses des bourgeons, un important groupe d'insectes défoliateurs, font partie intégrante de la dynamique naturelle des forêts nord-américaines (Harvey 1985). En forêt boréale mixte et coniférienne, la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) (Lepidoptera: Tortricidae) affecte d'ailleurs périodiquement et de façon importante la croissance du sapin baumier (*Abies balsamea* [L.] Mill.) et des épinettes (*Picea* spp.) en plus d'entraîner une mortalité

importante chez les individus matures de ces espèces-hôtes. Les taux de mortalité variables selon les différentes espèces-hôtes contribuent à créer une dynamique de trouées permettant ainsi à de nouvelles générations de végétation de gagner accès aux ressources (lumière, humidité, espace) jusqu'alors monopolisées par les strates dominantes (Kneeshaw et Bergeron 1998; 1999). C'est ainsi que les épidémies de la tordeuse de l'épinette (TBE) jouent un rôle important, tant au niveau de la succession forestière, que des cycles des éléments nutritifs et des patrons de diversité biologique. Bien que des épidémies localisées de tordeuses des bourgeons de l'épinette aient été rapportées pour les derniers millénaires, certains chercheurs postulent que celles-ci soient devenues plus fréquentes, plus sévères et aient affecté de plus grandes étendues au cours des deux siècles derniers (Blais 1983; Jardon *et al.* 2003; Simard *et al.* 2006). Il est logique que ce type de régime de perturbation subisse certaines fluctuations à l'intérieur d'une telle plage temporelle, mais ces mêmes chercheurs suggèrent que le régime actuel d'épidémies de TBE soit sans précédent, évoluant maintenant à l'extérieur de la plage de variabilité historique. La dernière épidémie de TBE, survenue entre le milieu des années 1970 et la fin des années 1980, étaient en effet la plus sévère depuis la tenue d'archives et a réduit l'approvisionnement en bois de plus de 25%, entraînant par le fait même d'importantes pertes socio-économiques (Power 1991; National Forestry Database 1995).

Les activités anthropiques ainsi que les changements climatiques, par l'entremise d'importants changements au niveau de la composition et de la structure des forêts, sont potentiellement responsables de cette modification au régime d'épidémies de TBE. Dans certaines parties de l'est du Canada, les aménagements forestiers (coupes, suppression des feux, pratiques sylvicoles, épandage d'insecticides) ont entraîné d'importantes modifications à la structure des paysages forestiers, faisant passer celui-ci d'une mosaïque très hétérogène de peuplements variés à une mosaïque beaucoup plus homogène dominée par des peuplements matures de sapins baumiers, extrêmement vulnérables aux épidémies de TBE (Bergeron *et al.* 1998). Une diminution de la fréquence des feux, résultant des conditions plus humides entraînées par les

changements climatiques (Flannigan *et al.* 1998) a peut-être aussi contribué à augmenter la prépondérance du sapin baumier.

Une meilleure compréhension de la relation entre la composition de la forêt et la sévérité des épidémies de TBE pourra expliquer certains processus-clés de la dynamique naturelle de la forêt boréale mixte et coniférienne. Elle devrait aussi permettre de mieux prévoir les impacts des changements climatiques tout en offrant la possibilité d'en atténuer les impacts socio-économiques des épidémies à venir.

Il a maintes fois été suggéré que la sévérité des épidémies de TBE varie en fonction de la composition forestière (MacLean 1980; Blais 1983; Bergeron *et al.* 1995). L'objectif principal de cette thèse est de tester cette hypothèse. J'ai évalué l'influence de la variabilité spatiale et temporelle de la composition forestière sur la sévérité des épidémies de TBE et proposé différents scénarios de voies successioneilles répondant aux divers niveaux de sévérité des épidémies. Une emphase particulière a été mise sur l'influence de la composition du paysage forestier environnant sur la sévérité des épidémies dans des peuplements matures de sapins baumiers et d'épinettes.

Cette étude a été effectuée dans deux régions distinctes, l'une dans la forêt boréale de l'Abitibi, dans le nord-ouest du Québec, et l'autre, en forêt mixte du nord du Nouveau-Brunswick. Les forêts de ces deux régions diffèrent considérablement, notamment au niveau de la diversité des espèces décidues, mais aussi en ce qui a trait à leur historique de perturbation et d'aménagement. On a en effet plutôt laissé libre cours aux épidémies de TBE dans le nord-ouest du Québec, tandis que d'importants programmes d'épandages d'insecticides ont été mis en opération au Nouveau Brunswick afin de minimiser les impacts des épidémies sur les réserves de bois. De plus, ce n'est que pendant les années 1970 qu'a débuté l'exploitation mécanisée intensive de la forêt et l'agriculture extensive Abitibi (Harvey et Bergeron 1989) alors que l'historique d'exploitation est beaucoup plus ancienne au nord du Nouveau Brunswick (Wein et Moore 1977). Les deux régions ont cependant connu une augmentation de l'abondance des espèces-hôtes de la TBE. Dans le cas de l'Abitibi, ceci a probablement été causé par la suppression des feux au cours des dernières décennies ainsi que par les changements

climatiques ayant eu lieu depuis la fin du Petit Âge Glaciaire (ca. 1850) (Bergeron et Dubuc 1989). Dans le cas du Nouveau Brunswick, l'augmentation de l'abondance des espèces vulnérables à la TBE a probablement plutôt été favorisée par l'épandage d'insecticides, ainsi que par la plantation d'essences résineuses plus vulnérables, puisque l'influence du feu y est historiquement moins importante qu'en Abitibi, les intervalles entre deux feux étant habituellement très longs (Wein et Moore 1977; Lauzon et al. 2007). Cette étude menée simultanément en Abitibi et au Nouveau Brunswick offre donc la possibilité unique d'examiner l'influence des épidémies de TBE dans deux contextes différents. Plus spécifiquement, je suis arrivée à mettre en évidence des patrons épidémiques distincts, j'ai aussi pu quantifier l'influence de l'épandage d'insecticides sur la sévérité des épidémies, tout en illustrant les interactions potentielles entre la sévérité des épidémies et l'historique des feux.

Bien que les épidémies de TBE ne peuvent pas être prévenues en raison des caractéristiques intrinsèques de leur dynamique des populations (Royama 1984; 2005), les aménagements forestiers peuvent être utilisés afin d'en atténuer les impacts (MacLean 1996; 2001). Le Système d'Aide à la Décision concernant la Tordeuse des Bourgeons de l'Épinette (SAD TBE), développé par le Service Canadien des Forêts (MacLean et Porter 1994) a en effet été conçu à cette fin. À ce jour, le SAD TBE a été implémenté à travers le Canada à l'aide de scénarios d'épidémies généralisés à partir de ceux développés pour le Nouveau Brunswick (*cf.* MacLean *et al.* 2001). Bien que les concepteurs de ce système d'aide à la décision reconnaissent qu'il y ait une importante variabilité intra- et inter-régionale au niveau des patrons épidémiques, celles-ci n'ont toujours pas été incorporées à cet outil de planification. L'objectif ultime de cette thèse était donc de considérer cette variabilité en incorporant de nouvelles données récoltées sur le terrain au sein de modèles simulant les impacts des épidémies futures pour un territoire pilote situé au Québec.

La présente thèse est subdivisée en cinq principaux chapitres (chapitres 2 à 6). Le thème central de celle-ci étant d'explorer la relation entre la composition forestière et la sévérité des épidémies, les différents chapitres traitent de ce thème en l'abordant sous

l'angle du temps et de l'espace, par l'entremise de plusieurs types de mesure de sévérité d'épidémie, tout en incorporant l'incontournable et confondante variable des aménagements forestiers. Les objectifs spécifiques de chaque chapitre sont les suivants:

Le chapitre 2, intitulé 'Spruce budworm outbreak dynamics in relation to bioclimatic conditions of boreal forests in Northwestern Québec', consiste en une reconstitution de l'occurrence des épidémies de TBE dans 16 peuplements âgés de la forêt boréale du nord-ouest québécois au moyen de méthode dendrochronologiques. Nous avons effectué cette reconstitution dans le but de décrire les relations entre les patrons temporels des épidémies de TBE et les variations du climat ainsi que de composition forestière.

Le chapitre 3, intitulé "Landscape structure and stand characteristics influence the severity of spruce budworm outbreaks in boreal forests", décrit l'influence de la composition des paysages environnants sur la sévérité de la suppression de croissance induite par les épidémies de TBE au sein de peuplements matures à co-dominance de sapins et d'épinettes. Cette étude a été effectuée dans la forêt boréale de l'Abitibi, dans le nord-ouest du Québec. Ici, nous y avons quantifié l'influence relative des caractéristiques locales des peuplements et de la composition du paysage environnant. Le design expérimental étant stratifié en fonction du temps depuis le dernier feu, on y inclut une discussion portant sur l'interaction entre feux et épidémies par l'entremise de leurs impacts respectifs sur la composition forestière.

Le chapitre 4, intitulé "Patterns of budworm-caused tree deaths in relation to the hardwood content of boreal forest landscapes" décrit l'influence de la proportion en espèces décidues des paysages environnants sur les patrons spatiaux-temporels de mortalité du sapin dans des peuplements à co-dominance de sapins et d'épinettes de l'Abitibi. Cette étude, avec les résultats sur les diminutions de croissance radiale dans la région d'Abitibi (Chapter 3), fournit des informations fondamentales sur les dynamiques des forest boreal affectée par des épidémies de TBE.

Le chapitre 5, intitulé "The severity of budworm-caused growth reductions vary with the hardwood content of surrounding landscapes" consiste en une quantification de

la relation entre la sévérité des épidémies de TBE dans des peuplements à co-dominance de sapins et d'épinettes du Nouveau Brunswick et la proportion environnante en espèces décidues dans un rayon de 1 km. On y discute aussi des effets potentiellement confondants de l'altitude et de l'historique d'épandage d'insecticides.

Le chapitre 6, quant à lui intitulé “ Implementing the Spruce Budworm Decision Support System in northwestern Quebec: incorporating forest hardwood content into stand vulnerability estimates” suggère une méthodologie permettant d'incorporer les informations sur la variabilité des patrons épidémiques dans les outils décisionnels permettant de prédire les impacts des épidémies de TBE à venir. Ces travaux de modélisation, implémentés pour la Forêt d'Enseignement et de Recherche du Lac Duparquet en Abitibi, résultent en une estimation des pertes potentielles de volume ligneux (en m^3/ha) pour 7 scénarios d'épidémies de TBE. La comparaison de ces scénarios montre de quelle façon l'ajout d'information sur les patrons épidémiques régionaux, notamment liés à la composition forestière, permet d'améliorer la précision des modèles prédictifs.

2 ARTICLE I - SPRUCE BUDWORM OUTBREAK DYNAMICS IN RELATION TO BIOCLIMATIC CONDITIONS OF BOREAL FORESTS IN NORTHWESTERN QUEBEC

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2.1 Résumé

La dendrochronologie a été utilisée pour reconstruire les épidémies de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) dans 16 peuplements âgés de la forêt boréale du nord-ouest québécois. Après avoir contrôlé pour le signal climatique inclus dans les cernes de croissance des arbres hôtes, épidémies ont pu être déduites à partir de plusieurs périodes prolongées de réduction de la croissance radiale chez *Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss: 1801-1813, 1823-1838, 1851-1867, 1881-1899, 1923-1934, 1937-1946, 1972-1987. L'estimation du temps de retour des épidémies était de 14-42 ans alors que la durée des épidémies était de 12-15 ans. L'épidémie caractérisée par des réductions de croissance entre 1923 et 1934 a été la plus sévère observée depuis les 200 dernières années. L'indice de l'oscillation Nord-Atlantique pour le mois de décembre expliquait une partie significative de la variance ($R^2 = 0.22$; $p = 0.005$) dans la fréquence des réductions de croissance causée par la tordeuse, suggérant que les hivers froids pourraient limiter la sévérité des épidémies. L'indice de sécheresse canadien du mois de juillet était lui aussi fortement associé à la fréquence des réductions de croissance ($R^2 = -0.56$; $p < 0.005$); la plupart des épidémies se sont produites durant des périodes humides. La plus sévère épidémie observée depuis les 200 dernières années (1923-1934) a été associée aux températures élevées d'hiver, aux périodes humides prolongées et à l'abondance des *Abies balsamea* matures.

Mot-cles: Tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*); dendrochronologie; sapin baumier; forêt boréale; reconstruction des épidémies d'insectes; variabilité du climat

2.2 Abstract

Dendrochronological techniques were used to reconstruct spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak dynamics in 16 old-growth stands in boreal forests of northwestern Quebec. Following removal of the climate signal from host tree ringwidths, budworm outbreaks were inferred from several prolonged periods of reduced radial growth in *Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss: 1801-1813, 1823-1838, 1851-1867, 1881-1899, 1923-1934, 1937-1946 and 1972-1987. Mean outbreak return-interval was about 29 years and mean outbreak duration 12-15 years. The outbreak inferred from growth reductions between 1923 and 1934 was the most severe over that last 200 years. North Atlantic Oscillation indices for December explained a significant amount of the variance ($R^2 = 0.22$; $p = 0.005$) in the annual frequency of budworm-caused growth reductions, suggesting cold winters may limit outbreak severity. Canadian Drought Code indices for July were also strongly associated with the frequency of budworm-caused growth reductions ($R^2 = -0.56$; $p < 0.001$), with almost all outbreaks occurring during prolonged wet periods. The most severe outbreak occurred when wet summers and warm winters (and springs) temperatures were coincident with abundant mature *A. balsamea* in stands and over landscapes.

Keywords: spruce budworm; dendrochronology; balsam fir; boreal forest; insect outbreak reconstruction; climate variability

2.3 Introduction

Native insect outbreaks play an integral role in the dynamics of forest ecosystems and the maintenance of biological diversity. Consumption of photosynthetic tissues by outbreaking defoliators has important implications for nutrient cycling, carbon sequestration, and the redistribution of biomass. Species-specific mortality induced by insects also alters competitive plant interactions and modifies forest structure and composition, accelerating the process of succession in some cases and restarting it in others (Schowalter 1981). In addition, insect outbreaks may strongly influence the probability of occurrence and severity of subsequent disturbances (Schmid and Mata 1996; McCullough et al. 1998).

Periodic outbreaks of a group of insects called budworms are natural disturbances of many North American forests. Spruce budworm (*Choristoneura fumiferana* Clem.) (Lepidoptera: Tortricidae) outbreaks have widespread impacts in fir-spruce stands eastern North America (Hardy et al. 1986). Emerging from overwintering hibernacula in May, spruce budworm larvae feed on the previous year's foliage and the expanding vegetative buds of *Abies balsamea* (L.) Mill. and *Picea* spp. Repeated annual defoliation during spruce budworm outbreaks diminishes cone production, causes reductions in host tree growth, and frequently kills a significant proportion of *A. balsamea* in stands (Bergeron et al. 1995). The creation of canopy openings due to overstory tree deaths following spruce budworm outbreaks promotes the release of seedling banks and recruitment of subcanopy trees into the main canopy (Morin 1994; Kneeshaw and Bergeron 1998). Abundant tree deaths caused by budworm also increase fuel loads and temporarily increase the probability of forest fires (Stocks 1987; Fleming et al. 2002).

Many have proposed that budworm outbreak dynamics have changed in eastern North America over the last 200 years. Aerial surveys of defoliation show the last outbreak of the 1970s and 1980s, which generated substantial economic losses in the

forestry industry, was more severe than the one recorded in the 1940s (Hardy et al. 1986). Two paleoecological studies of budworm macrofossil abundance have enabled the reconstruction of budworm outbreaks over millennia, indicating that they were uncommon events until the 20th century (Simard et al. 2006). A number of dendrochronological studies that have reconstructed the history of spruce budworm outbreaks over the last 200 to 450 years indicate an increase in the frequency, duration, intensity and extent of outbreaks (Blais 1981; Jardon et al. 2003; Morin and Laprise 1990; Morin et al. 1993). These findings are consistent with dendrochronological studies that report temporal changes in outbreak dynamics for other defoliators: *Choristoneura occidentalis* (Swetnam and Lynch 1993), *Zeiraphera diniana* (Weber 1997), *Coloradia pandora* (Speer et al. 2001).

Human land-use activities and global climate change are likely to generate profound shifts in natural disturbance regimes, particularly the dynamics and impacts of insect outbreaks, some of which we are already seeing (Roland et al. 1993; Ayres and Lombardo 2000). The changes in spruce budworm outbreak patterns reported above have been attributed to a greater abundance and continuity of host trees in stands and over landscapes caused by fire suppression, silvicultural practices and insecticide spraying (Blais 1983). Defoliator outbreaks have typically been associated with host stress during droughts (Mattson and Haack 1987) and it has been proposed that warming temperatures associated with climate change could exacerbate this situation (Dale et al. 2001). On the other hand, Swetnam and Lynch (1993) report budworm outbreaks associated with periods of wetter than average weather in Colorado. Warmer winters associated with climate change could increase budworm over-wintering survival and alter species interactions that drive the dynamics and impact of outbreaks (Candau and Fleming 2005; Hance et al. 2007; van Asch and Visser 2007). Understanding relationships between historical outbreak patterns and climate variability can provide significant insight into the potential effects of climate change.

Tree-ring reconstructions of insect outbreak history can provide valuable information about the trends in defoliator outbreak events and generate a basis from

which to evaluate the potential impacts of changing climate and forest composition. While a number of tree-ring reconstructions indicate substantial changes in spruce budworm outbreak patterns over the 20th century, particularly an increase in frequency and extent (Blais 1981; Morin and Laprise 1990; Morin et al. 1993) others report no such trends (Jardon et al. 2003; Boulanger and Arsenault 2004). A plethora of methodological and analytical differences among tree-ring studies, as well as the presence of confounding variables, may account for the apparent inconsistencies among tree-ring reconstructions. Among comparisons of tree-ring reconstructions throughout Quebec, Boulanger and Arsenault (2004) indicated that those from western Quebec (e.g., Morin et al. 1993) were most distinct particularly with respect to their timing and duration. Using an independent data set that had a larger number of samples, and analytical methods more similar to Boulanger and Arsenault (2004), the first objective of our study was to re-assess historical outbreak patterns for the same area in which Morin et al. (1993) conducted their study in western Quebec. Our second objective was to examine relationships between temporal variability in bioclimatic conditions and outbreak dynamics, as none of the outbreak reconstructions to date address this. Thus, the aim of this study was to test two hypotheses: i) budworm outbreak patterns have changed over last 200 years in western Quebec and ii) temporal variability in climate and forest composition explains variations in budworm outbreak patterns over the last two centuries.

2.4 Study Area

The study area is located near the southern limit of the Canadian boreal forest, close to the Québec-Ontario border (48°30'N, 79°25'W) (Fig. 2.1). In this area, hills covered by moraine deposits alternate with lowlands covered by clays from post-glacial lakes (Vincent and Hardy 1977). Weather station data (35 km north of Lac Duparquet) indicate a continental climate with a mean annual temperature of 0.6°C, mean annual precipitation of 822.7 mm, and a mean annual frost-free period of 64 days, although

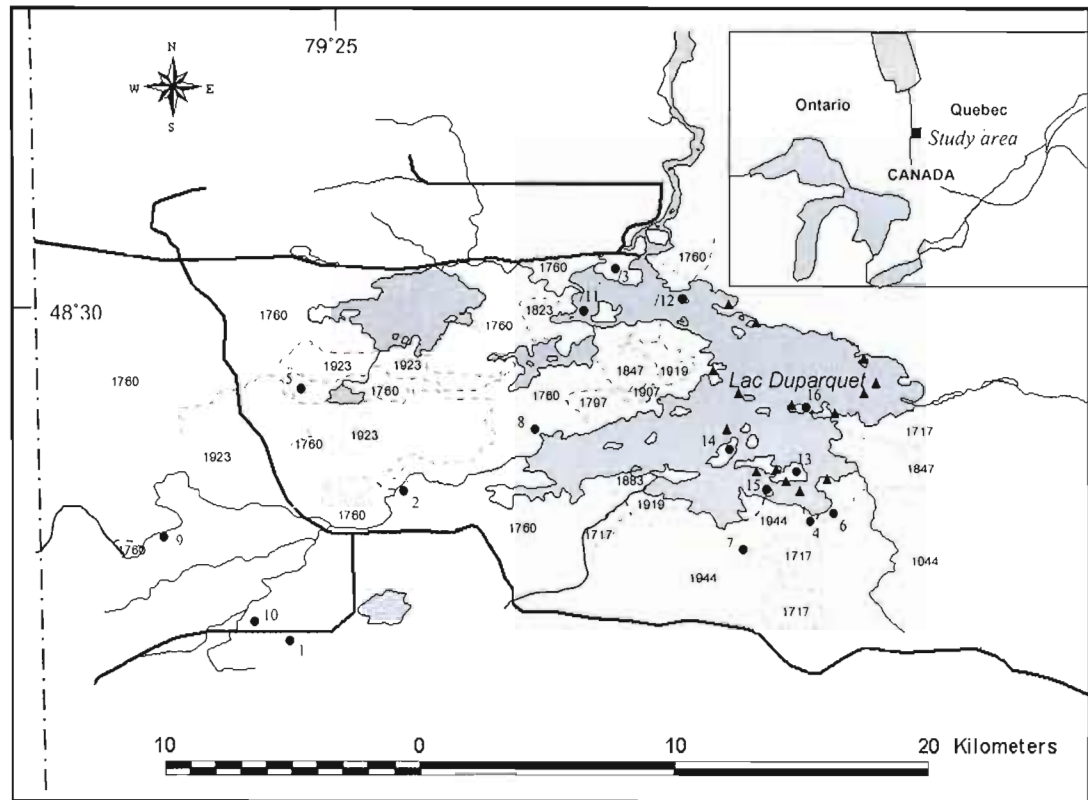


Figure 2.1. Location of 16 sampled stands (●). Tree-ring data obtained from non-host sites (▲) sampled in a previous study (Archambault and Bergeron 1992). Fire areas are indicated by dashed grey lines and approximate burn year (from: Dansereau and Bergeron 1993).

freezing temperatures can occur any time throughout the year (Environment Canada 2002).

Forest composition in the study area depends on surficial deposits and successional stage (Bergeron and Bouchard 1983; Bergeron 2000). On mesic sites with clay deposits, post-fire stands (<100 years old) are dominated by *Populus tremuloides* Michx., mid-seral stands (100-200 years) by *A. balsamea*, *Betula papyrifera* Marsh., and *P. glauca*, and late-seral stands by *A. balsamea* and *T. occidentalis*, with a lesser component of *P. glauca*. On drier sites with moraine deposits, *B. papyrifera* dominates early successional stands. Mid-seral and late-successional stands are dominated by the same species that occur on clay deposits but these drier sites usually have more *Picea mariana* (Mill.) B.S.P. than *P. glauca*. Early and mid-successional stands on bedrock are dominated by *P. mariana* and *Pinus banksiana* Lamb. or *P. resinosa* Ait., with *T. occidentalis* becoming more abundant as stands age. Bogs and other hydric sites are dominated by *P. mariana*, *T. occidentalis*, and *Larix laricina* (Du Roi) K. Koch. *Fraxinus nigra* Marsh. and *Ulmus americana* L. dominate floodplains.

Fire has occurred throughout the area, with the most recent stand-replacing fires occurring in 1923 and 1944, and the oldest records of fires in 1717 and 1760 (Dansereau and Bergeron 1993). The last spruce budworm outbreak in this region occurred from 1971-1985 (Ressources naturelles Québec, *unpublished aerial survey data*). Human land-use activities include forestry, mining and farming but they are restricted to the northern part of the study area, which is more populated.

2.5 Materials and Methods

Sixteen old-growth stands were sampled on forested sites undisturbed by fire for at least 238 years (Fig. 2.1). In each stand, two increment cores were extracted from at least 10 of the largest, and apparently, the oldest *A. balsamea* and *P. glauca*. Cores were taken from the base (< 30 cm above the germination point) on opposite sides of the tree. Basal disks cut from any portion of the undecayed bole below breast height 1.3 m, were

also collected from dead *A. balsamea*. As *P. glauca* is rarely killed by budworm outbreaks in our study area, no basal disks were taken from this host species.

All increment cores and basal disks collected from *A. balsamea* and *P. glauca* were prepared in the laboratory following standard dendrochronology procedures (Swetnam et al. 1985). After sanding and mounting of cores, tree rings were visually cross-dated within plots, using a modified skeleton plot method (Yamaguchi 1991) and measured to the nearest 0.001 mm using a Velmex™ Uni Slide Micrometer connected to a computer. The program COFECHA (Holmes 1983) was used to verify dating. Tree-ring series that did not cross-date well with other samples in the stand (i.e., $r < 0.350$) were checked for dating or measurement errors and corrected as necessary. Series that remained poorly correlated with other samples were then eliminated from the dataset of each stand. On average, 11% of the series were removed. All raw tree-ring series were then standardized to remove long-term, age-related growth trends using the program ARSTAN (Cook 1985). Following Boulanger and Arsenault (2004), standardization was achieved by a cubic smoothing spline with a 50% frequency response of 60 years. The resulting standardized tree-ring series were comprised of dimensionless ring-width values where 1.0 is equivalent to mean tree growth, values >1.0 represent above-average growth and values <1.0 indicate growth reductions. Standardized tree-ring series were averaged to produce a mean tree-ring chronology for each stand. Dating and standardization procedures were applied separately to each host species.

The program OUTBREAK (Holmes and Swetnam 1996) was used to automate the procedure of identifying growth reductions attributed to past budworm outbreaks. To enhance the detection of budworm outbreaks in host tree-ring chronologies, we first used OUTBREAK to remove climate variation in individual host tree-ring series through subtraction of a standardized non-host chronology, which we constructed from previously collected tree-ring data for 39 *Thuja occidentalis* collected over 15 sites in our study area (Fig. 2.1) (Archambault and Bergeron 1992). Because effective application of this ‘correction’ procedure assumes similar host and non-host growth responses to climate fluctuations (Swetnam et al. 1985), we tested for this prior to

OUTBREAK runs using temperature and precipitation data obtained from nine weather stations within 200 km of the study area (Environment Canada 2002) and simple Pearson correlations and bootstrapped response function analysis procedures in PRECON (Fritts 1999).

After non-host chronologies were subtracted from host chronologies, we set the OUTBREAK program to attribute growth reductions to budworm outbreaks if: i) portions of the corrected tree-ring series had reduced growth for greater than 5 years; and, ii) at least one year of reduced growth in this period was at least -1.28 standard deviation units. Even though previous work suggests that these criteria are sufficient to detect historical budworm outbreaks in tree rings (Swetnam et al. 1985; Jardon et al. 2003; Ryerson et al. 2003), we used aerial sketch maps of modern budworm outbreaks (from 1938 to 1987) to assess our ability to detect outbreak in tree rings.

OUTBREAK was run on mean tree-ring chronologies for each stand and then on individual tree-ring series for each stand as well as a pooled dataset of individual tree-ring series over all stands in the study area. OUTBREAK runs for individual tree-ring series were used to generate frequency distributions of the percentage of budworm-affected trees. In addition to OUTBREAK runs on mean chronologies, these frequency distributions helped to characterize spruce budworm outbreak dynamics (i.e., outbreak occurrence, severity, duration, return-interval, and extent) over the last 200 years in the study area. Outbreaks were considered to occur in each stand, and over the study area, if synchronous periods of reduced growth affected $\geq 30\%$ of host trees. Outbreak severity was considered light if between 30% and 60% of trees had reduced growth and severe if $\geq 60\%$ of host trees were affected. Outbreak duration was defined as the number of consecutive years with $\geq 30\%$ of host trees having growth reduction and outbreak return interval was calculated as the period of time between the start year of one outbreak and the start year of the next outbreak. Outbreak extent was defined as the proportion of sample stands having a budworm outbreak.

2.5.1 Outbreak dynamics in relation to variations in bioclimatic conditions

Relationships between spruce budworm outbreak patterns and climate were investigated by comparing tree-ring reconstruction of budworm outbreaks over the last 200 years with historic climate conditions. Because weather records in our study region extend only as far back as 1896, instrumental records of the North Atlantic Oscillation (NAO), which span 1823 to 2007 (Luterbacher et al. 2001), were used to explore relationships between outbreak occurrence and severity (% affected hosts) in relation to winter temperatures. The NAO is a dominant pattern of atmospheric circulation that influences winter climate. Comparisons of NAO indices (Luterbacher et al. 2001) with weather station data in the region of our study area (Environment Canada 2002) indicate a strong association with annual temperatures fluctuations in December and January (Pearson coeff.: $p < 0.05$). The negative, or low, phases of the NAO are associated with cold winters. NAO indices for December and January were compared to frequency distributions of budworm-affected *A. balsamea* and *P. glauca*. To explore relationships between host drought stress and outbreak occurrence or severity, frequency distributions of budworm-affected trees were compared to independent tree-ring construction of the July Canadian Drought Code index (CDC) for our study area (Girardin et al. 2004). Simple regression analysis was used to test for relationships between the percentage of budworm affected trees and indices of NAO and jCDC.

Tree establishment and death dates, which formed the basis of work on post-fire succession in our study area (Bergeron 2000), were used to assess relationships between outbreak severity and temporal variability in the abundance of the budworm's primary host, *A. balsamea*. Because data on host abundance was compiled in relation to time since a 1760 wildfire in our study area, we compared frequency distributions of budworm-affected trees to *A. balsamea* abundance for a subset of stands, that is, combined tree ring data from stands H1, H2, H3, H5, H8, H9, H10) that originated from the 1760 wildfire (Fig. 2.1; Dansereau and Bergeron 1993).

2.6 Results

2.6.1 Dendrochronological characteristics

A total of 731 tree-ring series, from 18 to 54 host trees (*A. balsamea* and *P. glauca*) per stand and 42 non-host trees (*T. occidentalis*), were used to construct mean standardized chronologies of radial growth and identify spruce budworm outbreaks over about the last 200 years in 16 stands (Table 2.1). Raw ringwidth measurements (mm) indicated that *A. balsamea* grew slower than *P. glauca*, and had more absent rings (primarily between 1981-1987). *T. occidentalis* grew at least 60 percent slower than either of the budworm hosts. Despite overall differences in tree growth rates, cross-dating, plot overlays, and Pearson correlations ($R = 0.38$ to 0.80 ; for the 12-year segment of tree ringwidth prior to the 1970s/80s budworm outbreak) indicated that high-frequency interannual variations in tree-ring widths corresponded well between the host chronologies for each stand and the composite non-host chronology. Common growth patterns among trees in each stand is reflected in the strong inter-radii correlations for host species, and also by a substantial percentage of the variation in radial growth being explained by the first eigenvector of a principal components analysis on tree ring series of ringwidth (conducted by ARSTAN). Plots of correlation functions for each stand indicated that overall host and non-host growth responses to annual fluctuations in precipitation and temperature were highly similar (Table 2.2; Fig. 2.2).

For all species, reductions in annual growth ring widths were associated with high temperatures in June, July or August of the previous year, and current year of growth (Table 2.2; Fig. 2.2). *T. occidentalis* had more statistically significant negative relationships between growing season temperatures and ring width than host trees, suggesting greater sensitivity to high temperatures. Longer growing seasons due to above average spring (March, April, May) temperatures were associated with increased ring widths, particularly for *P. glauca*. Above average precipitation late in the current growing season (August to October), and in June of the previous growing season was associated with larger tree-ring widths of all species in all stands (e.g., Fig. 2.2).

Table 2.1. Tree-ring chronology statistics for *Abies balsamea*, *Picea glauca*, and *Thuja occidentalis* in northwestern Quebec.

Stand	Spp. ¹	Chronology length	# radii	# trees	Mean raw ringwidth (mm)	% absent rings	Pearson correlation among radii	Variation in 1 st eigenvector (%)
n/a ³	To	1780-1987	47	39	0.36	0.02	0.341	37
H1	Ab	1897-1999	18	15	1.27	0.20	0.557	59
	Pg	1858-1998	18	11	1.25	0.00	0.279	34
H2	Ab	1892-1998	54	33	1.50	0.28	0.491	52
	Pg	1850-1998	39	21	1.88	0.00	0.328	36
H3	Ab	1888-1998	48	27	1.56	0.11	0.612	63
	Pg	1833-1998	20	10	1.59	0.00	0.250	32
H4	Ab	1880-1998	25	13	1.51	0.45	0.561	59
	Pg	1782-1998	11	8	1.95	0.07	0.347	43
H5	Ab	1857-1998	23	12	1.65	0.00	0.560	60
	Pg	1780-1999	18	8	2.44	0.22	0.584	62
H6	Ab	1865-1999	29	16	1.49	0.18	0.555	59
	Pg	1867-1999	18	10	1.33	0.06	0.340	41
H7	Ab	1899-1999	31	15	1.71	0.00	0.416	51
	Pg	1824-1999	13	8	1.19	0.05	0.417	49
H8	Ab	1887-1999	17	9	1.61	0.00	0.339	39
	Pg	1805-1999	12	9	1.45	0.15	0.352	49
H9	Ab	1855-2000	17	13	1.40	0.00	0.251	35
	Pg	1816-2000	11	8	1.15	0.15	0.236	34
H10	Ab	1846-1993	14	10	1.32	0.00	0.457	51
	Pg	1821-2000	14	8	1.44	0.00	0.453	50
H11	Ab	1852-2000	22	15	1.00	0.13	0.235	34
	Pg	1834-2000	19	12	1.04	0.04	0.209	27
H12	Ab	1901-2000	22	14	1.51	0.07	0.477	52
	Pg	1842-2000	12	9	0.99	0.00	0.400	48
H13	Ab	1868-1986	26	16	1.24	0.05	0.231	31
	Pg	1849-2000	16	10	1.15	0.00	0.399	48
H14	Ab	1908-2000	23	15	1.41	0.00	0.369	49
	Pg	1821-2000	18	10	1.46	0.00	0.364	41
H15	Ab	1848-2000	34	22	1.14	0.24	0.280	34
	Pg	1827-2000	21	11	1.07	0.00	0.355	38
H16	Ab	1900-2000	24	17	1.24	0.00	0.299	37
	Pg	1783-2000	10	5	1.90	0.00	0.215	34

¹ Tree species: To= *Thuja occidentalis* (non-host), Ab=*Abies balsamea*, Pg=*Picea glauca*. ² standard deviation from mean ringwidth for standardized chronologies, which by definition is ~1.00.

³ Chronologies combined from multiple sites visited by Archambault and Bergeron (1992).

Table 2.2. Pearson correlation coefficients indicating the strength of relationships between temperature and precipitation response functions for hosts (*Abies balsamea* and *Picea glauca*) and climate response for the non-host (*Thuja occidentalis*). Coefficients of determination (R^2 -values), resulting from response function analysis indicate the proportion of variability in host tree ring widths that is explained by climate, that is, monthly temperature and precipitation (from May of the previous year [pM] to October of the current year [O]) between 1894-1993 for each of the 16 stands sampled.

Stand #	<i>Abies balsamea</i>					<i>Picea glauca</i>				
	Temperature (°C)		Precipitation (mm)		R^2	Temperature (°C)		Precipitation (mm)		R^2
	R		R			R		R		
H1	0.349	*	0.400	*	0.30	0.324	n/s	0.030	n/s	0.38
H2	0.473	***	0.568	**	0.30	0.457	**	0.013	n/s	0.32
H3	0.409	**	0.694	***	0.24	0.523	***	0.311	n/s	0.44
H4	0.515	***	0.401	**	0.34	0.552	***	0.115	n/s	0.50
H5	0.431	**	0.121	n/s	0.28	0.417	**	0.461	*	0.28
H6	0.304	n/s	0.430	**	0.27	0.321	n/s	0.225	n/s	0.37
H7	0.413	**	0.034	n/s	0.28	0.633	***	0.067	n/s	0.18
H8	0.224	n/s	0.368	*	0.28	0.506	***	0.133	*	0.36
H9	0.350	*	0.487	**	0.37	0.420	**	0.585	**	0.37
H10	0.610	***	0.299	n/s	0.27	0.526	***	0.417	**	0.27
H11	0.402	**	0.243	n/s	0.41	0.405	**	0.609	***	0.46
H12	0.539	***	0.543	***	0.35	0.534	**	0.650	***	0.35
H13	0.621	***	0.581	***	0.24	0.623	***	0.611	***	0.24
H14	0.407	**	0.581	***	0.39	0.698	***	0.682	***	0.39
H15	0.229	n/s	0.770	***	0.25	0.606	***	0.682	***	0.44
H16	0.043	n/s	0.270	n/s	0.34	0.658	***	0.116	n/s	0.38
Average	0.395		0.424		0.31	0.513		0.357		0.36

* $p=0.10-0.15$; ** $p=0.05-0.09$;

*** $p<0.05$

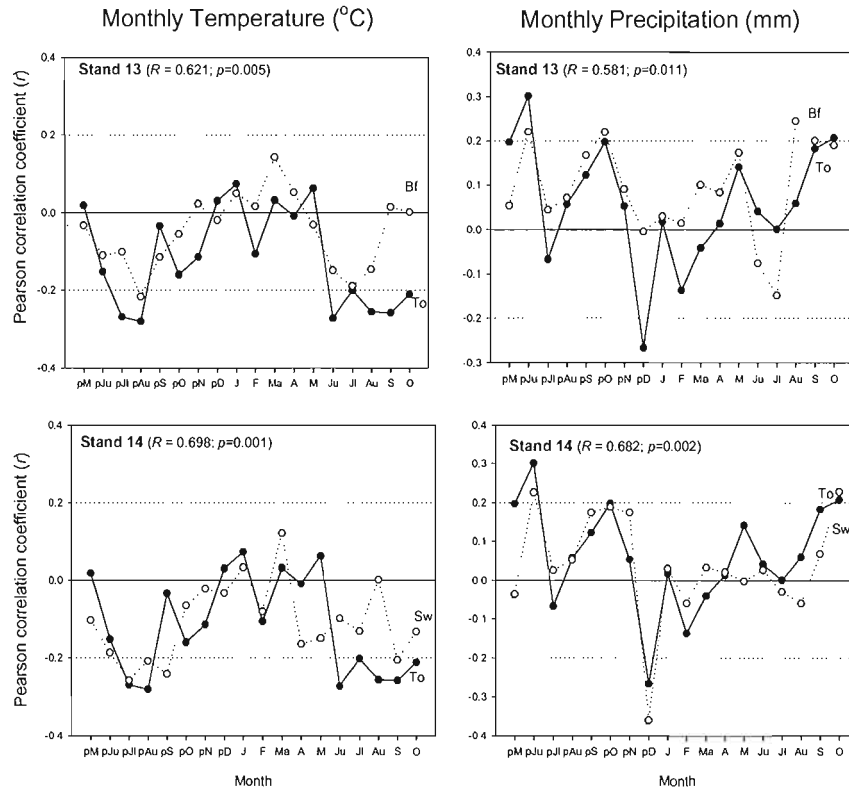


Figure 2.2. Examples comparing temperature and precipitation correlation function curves for budworm hosts (dashed line) and the non-host *Thuja occidentalis* (solid line) in two stands H13 and H14. Pearson correlations are given for relationships between radial growth and temperature or precipitation from January [J] to October [O] of the current year and May (pM) to October (pO) of the previous year.

2.6.2 Outbreak reconstruction from tree-ring records

Using frequency distributions of affected *A. balsamea*, we identified 5 periods of reduced host growth that could be attributed to spruce budworm outbreaks: 1851-1867, 1881-1897, 1923-1934, 1937-1946, and 1972-1987 (Fig. 2.3). The number of years between the start dates of successive outbreak periods was used to calculate the mean outbreak return interval for the study area, which was 30 years (range 14 to 42 years). Even though our ability to estimate the duration of the last budworm outbreak was limited by the end date of the non-host chronology used to correct host tree-ring series, we included it in our calculation of mean outbreak duration, which was 15 years. The budworm outbreak starting in 1923 appeared to be the most widespread and severe one, with more than 80% of host trees being affected. This outbreak was immediately followed by a second outbreak wave that occurred between 1937 and 1946 in fewer stands. *A. balsamea* radial growth reduction patterns indicated an alternating pattern of light ($\geq 30\%$ of host trees affected) and severe ($\geq 60\%$ of host trees affected) outbreaks over about the last 140 years. Some localized outbreaks may have occurred between 1897 and 1922 (Fig. 2.3) but small sample sizes, due to short *A. balsamea* tree-ring chronologies, make it difficult to attribute synchronous growth reductions to budworm outbreaks in individual stands.

Because *P. glauca* generally survived successive budworm outbreaks in our study area we were able to construct longer tree ringwidth chronologies for this species (Fig. 2.4). Using the frequency distributions of affected *P. glauca* trees, we identified 7 periods of reduced growth that could be attributed to budworm outbreaks over the last two centuries: 1801-1813, 1823-1838, 1855-1865, 1883-1899, 1923-1934, 1937-1945, 1972-1987 (Fig. 2.4). Mean outbreak return interval was 28 years (range 14 to 40 years) and mean outbreak duration 13 years (range 9-17 years). As tree-ring patterns indicated for *A. balsamea*, the outbreak starting in 1923 was the most severe — synchronous host growth reductions occurred in all stands, and more than 80% of trees over the study area were affected. The second outbreak wave that occurred

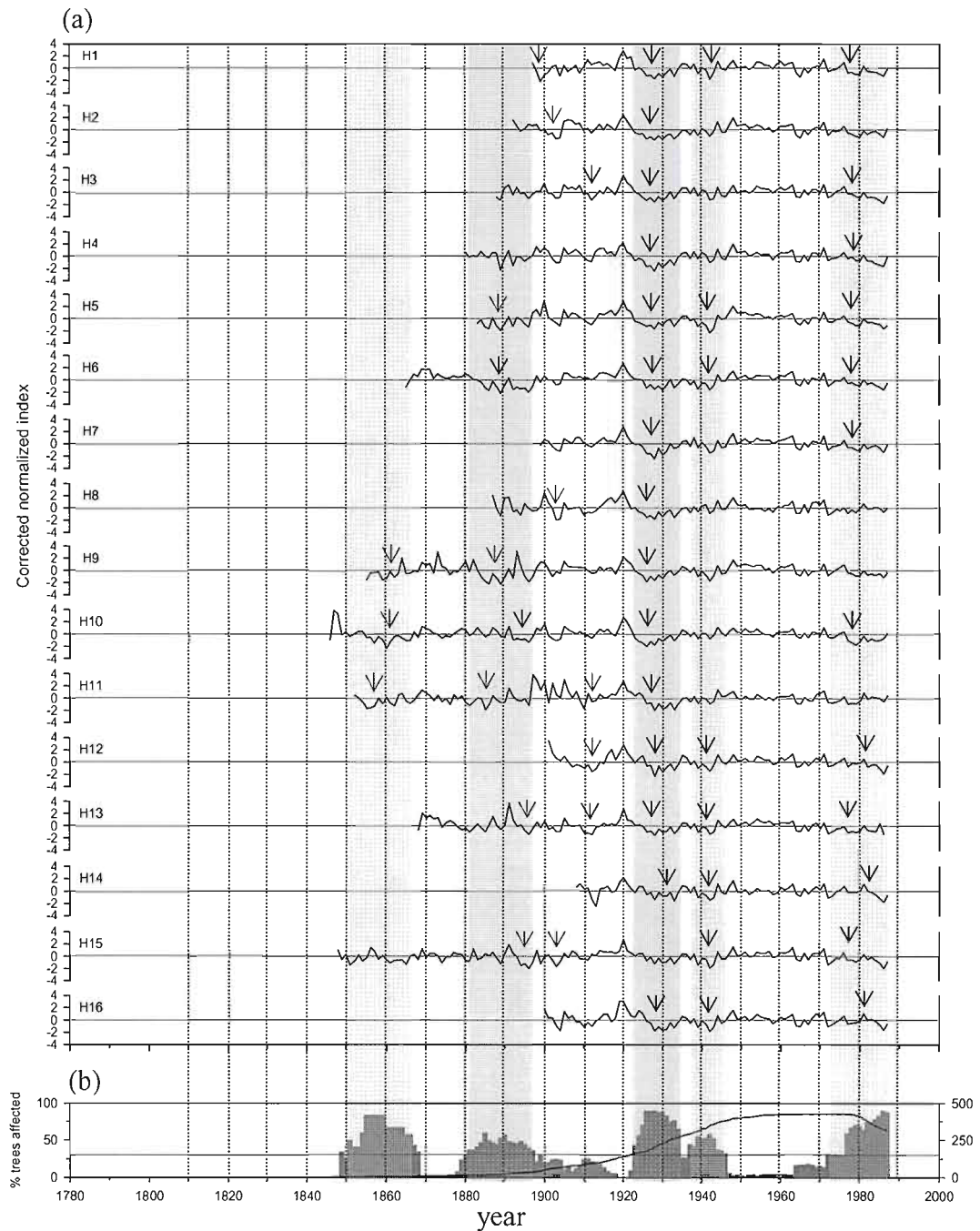


Figure 2.3. (a) Mean standardized chronologies of *A. balsamea* radial growth for 16 stands sampled in northwestern Quebec following subtraction of the climate signal. Black arrows budworm outbreaks; grey arrows indicate outbreaks inferred from less than 3 trees. (b) the percentage of affected *A. balsamea* trees over the entire study area. Vertical bars indicate outbreak periods (i.e., $\geq 30\%$ of host trees with reduced growth; solid horizontal line).

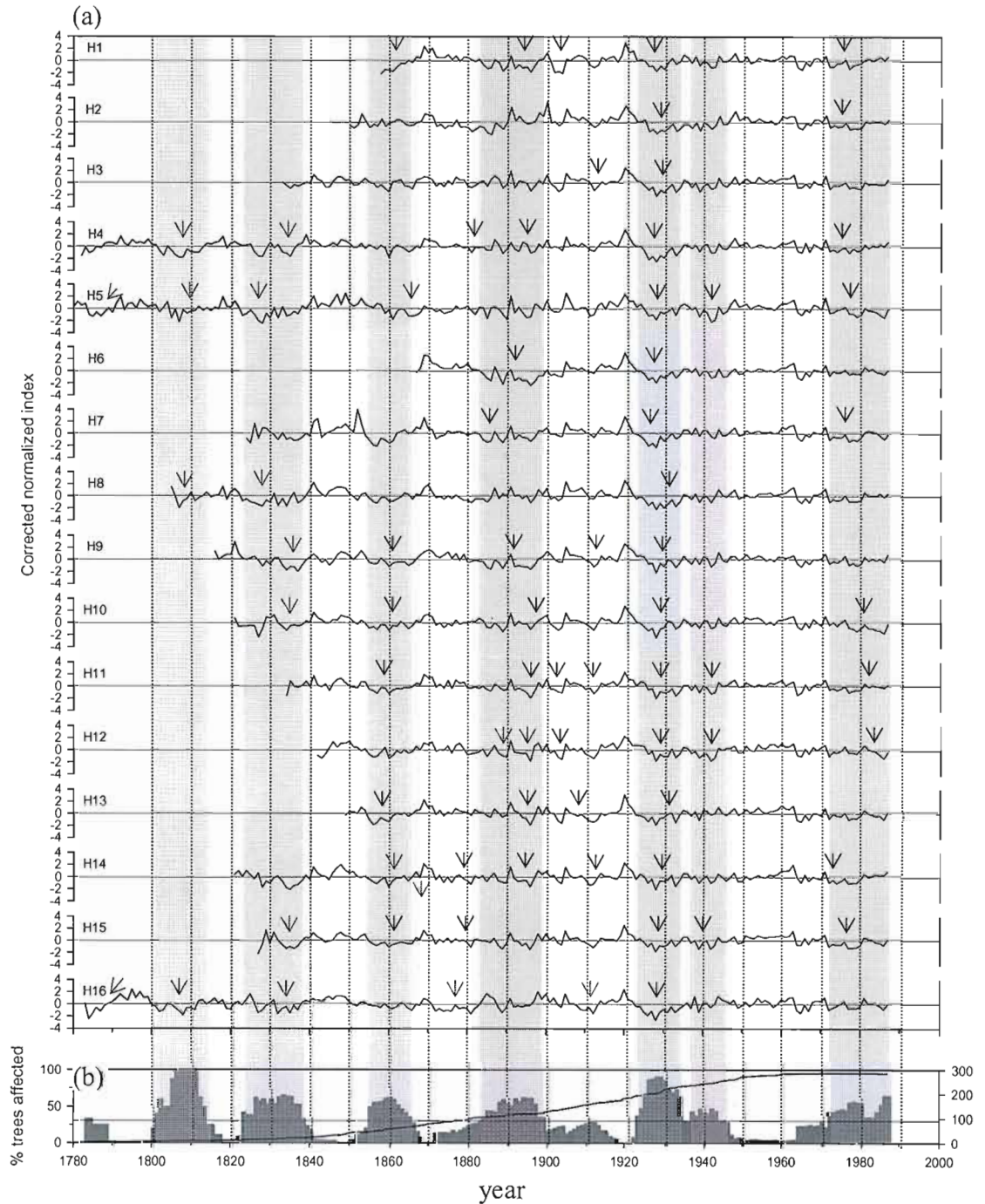


Figure 2.4. (a) Mean standardized chronologies of radial growth for 16 stands sampled in northwestern Quebec following subtraction of the climate signal. Black arrows indicate budworm outbreaks; grey arrows indicate outbreaks inferred from less than 3 trees. (b) the percentage of affected *P. glauca* trees over the entire study area. Vertical bars indicate outbreak periods (i.e., $\geq 30\%$ of host trees with reduced growth; solid horizontal line).

immediately after, from 1937-1945 was light (i.e., between 30-60% of trees affected) (Fig 2.4). Unlike *A. balsamea* tree-ring growth patterns, the only other severe outbreak indicated in *P. glauca* growth reductions occurred from 1801-1813, and this may be an artifact of small sample size. Like *A. balsamea* tree patterns, those of *P. glauca* that were based on larger sample sizes, indicate growth reductions that could be due to localized budworm outbreaks 1897 and 1923.

2.6.3 Budworm outbreak pattern and bioclimatic variability

Because *P. glauca* tree ring chronologies enabled reconstructions of outbreak history over a longer period of time than those of *A. balsamea*, and because each of the outbreak periods inferred from tree rings were the same using either species, frequency distributions of *P. glauca* were used to assess relationships between budworm outbreak patterns and bioclimatic variability.

Instrumental records indicated that three distinct positive December NAO phases, associated with warmer than average December temperatures, occurred over the last 170 years: 1830-1868, 1876-1957, and 1975-2000 (Fig 2.5a). Two negative phases associated with colder than average winter temperatures occurred from 1869-1875 and from 1958-1974. Simple linear regression analysis indicated that a significant amount of the variation in the frequency of *P. glauca* with radial growth reductions was associated with variation in December NAO indices ($R^2=0.22$; $p=0.005$) (Fig. 2.5). Except for the start of the last outbreak (1972-1979), all budworm outbreaks (i.e., periods of time when >30% of host trees had reduced growth) occurred during positive phases of the NAO (Fig. 2.5). The start of the most severe outbreak of the last two centuries (1923-1934) coincided with high December NAO indices and the second less severe outbreak wave immediately following (1937-1946) occurred when NAO indices had abruptly dropped by about half.

Inter-annual fluctuations in July CDC indices were greatest between 1862 and 1902. Outside of this period, longer periods of above average July CDC indices, indicating drier than average conditions, occurred from: 1813-1821, 1839-1849, 1914-1923, and

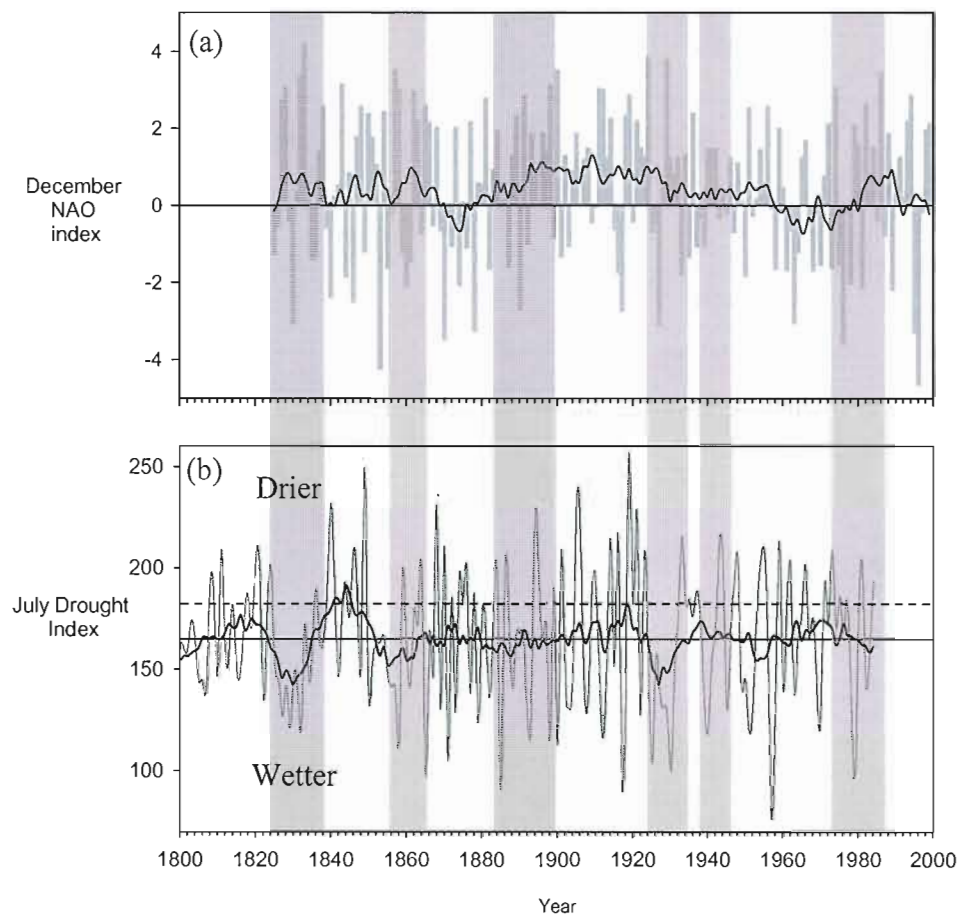


Figure 2.5. Budworm outbreak occurrence in relation to (a) the North Atlantic Oscillation (NAO) for December and (b) the Canadian Drought Code for July (Girardin et al. 2004). Average July drought conditions; values over 200 (dashed line) indicate dry conditions. Grey vertical bars indicated outbreak periods inferred from radial growth reductions of *Picea glauca*.

1965-1973 (Fig. 2.5b). Simple linear regression indicated a strong relationship between July CDC index values and the percentage of budworm-affected *P. glauca* trees ($R^2 = -0.56$; $p < 0.001$). All outbreaks occurred during wet periods (i.e., the drought index was below average) (Fig. 2.5b).

Forest composition in our study area varied over time within the old-growth stands sampled and in the surrounding the landscape. Overall, there was a near linear increase in the abundance of *A. balsamea* among stands originating from the 1760 wildfire (Fig. 2.6a). A concomitant linear increase in the frequency of budworm-affected spruce did not occur (Fig. 2.6b). Peaks in *A. balsamea* deaths and recruitment occurred from 1830-1850 and 1920-1934 indicating, mature trees vulnerable to outbreaks (i.e. >60 years-old) occurred most abundantly around 1910, 13 years prior to the 1923 outbreak, and then again at the time of the last outbreak in 1972-1987. Over the entire study area, major reductions in old *A. balsamea* forests occurred before the last two budworm outbreaks when large fires in 1923 and 1944 (Fig. 2.1) generated new early successional deciduous-dominated forests in the landscape surrounding the old-growth stands we sampled (also see Archambault and Bergeron 1992; Bergeron et al. 2000).

2.7 Discussion

2.7.1 Reliability of outbreak reconstructions from tree rings

Studies of tree-ring growth reduction patterns provide a means to study long-term outbreak patterns of phytophagous insects, particularly those with long population cycles. However, some studies indicate that dendrochronological methods may detect outbreaks that did not occur (i.e., “false” outbreaks) and fail to detect outbreaks in tree-rings when they actually did occur (Ryerson et al. 2003). Determining the precise timing of outbreaks can also be problematic (Speer et al. 2001; Parish and Antos 2002).

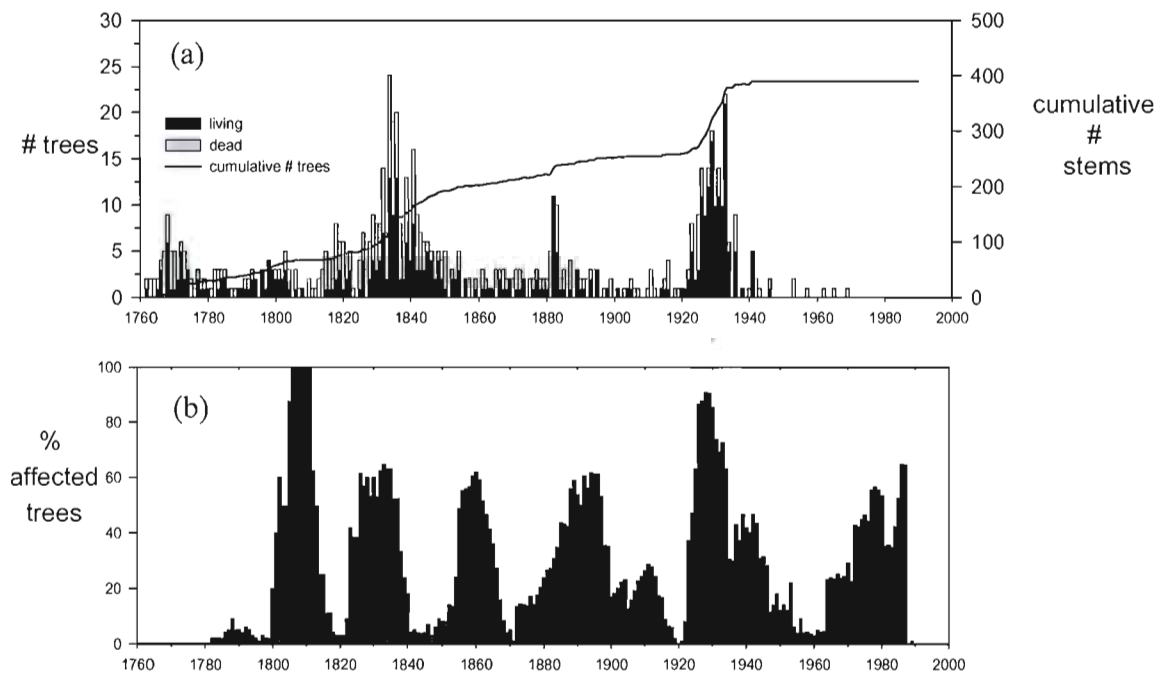


Figure 2.6. (a) Number of *A. balsamea* establishing (solid bars) or dying (open bars) each year and cumulative abundance of living *A. balsamea* (> 1 m in height) since 1760 (solid line). To indicate the overall trend, cumulative *A. balsamea* abundance is smoothed by a quadratic function (b) the percentage of budworm-affected *Picea glauca* since 1760 (dotted line marks 30% affected trees and level above which outbreaks were considered to have occurred).

The reliability of our budworm outbreak reconstructions was assessed through comparisons with: i) aerial sketch maps of budworm-caused defoliation (1938 to present); ii) somewhat less accurate cartographic representations of spruce budworm outbreaks (1909-1996); and iii) independent tree-ring reconstructions of budworm outbreaks in Quebec.

Budworm outbreaks from 1940-1950 and from 1971-1985 in the Abitibi region are well documented in aerial surveys of budworm-caused defoliation (Ministère des ressources naturelles et de la faune, 2006). Both of these outbreaks were detected in the tree rings of *A. balsamea* and *P. glauca*. However, the start and end dates of the outbreaks were in error by one to four years, with outbreaks inferred from tree rings occurring from 1938-1946 and from 1972-1987. A delay in growth responses to defoliation, as well as a period of growth recovery following defoliation cessation, likely explains the discrepancies in outbreak timing among tree-ring reconstructions and aerial survey data (Fritts 1976; Parish and Antos 2002). Tree-ring reconstructions using *A. balsamea* indicated more severe outbreaks than those using *P. glauca*. This is likely because *A. balsamea* is more vulnerable to defoliation than *P. glauca* — combined with the fact that budburst is more synchronous to the budworm's feeding cycle, *A. balsamea* also does not produce as much secondary foliage, or epicormic shoots, as *P. glauca* in response to defoliation (Nealis and Régnière 2004).

From 1900 to 1938, tree-ring reconstructions of budworm outbreaks were compared to older, less accurate cartographic representations of budworm outbreaks and other dendrochronological reconstructions of budworm outbreaks in Quebec. Tree-ring reconstructions indicated that a severe outbreak occurred from 1923 to 1934 in our study area. These findings corresponded well with Brown (1970), who observed severe infestations occurring in the region from 1923-1926, and previous dendrochronological studies in our study area (Morin et al. 1993) that attributed radial growth reductions to a budworm outbreak between 1919 and 1938. Another dendrochronology study in western Quebec, attributed growth reductions from 1906-1930 to a budworm outbreak (Jardon et al. 2003).

Prior to 1900, documentary archives of budworm do not exist and outbreaks must be inferred from tree-ring data. In this study, four periods of reduced host growth were attributed to budworm outbreaks: 1881-1899, 1851-1867, 1823-1838, and 1801-1813. As budworm outbreaks tend to be relatively synchronous over large regions (Gray et al. 2000), comparisons of these findings with the results of other dendrochronology studies yield some information about the probability of having correctly identified a past budworm outbreak. Our findings were compared to seven other studies: three in western Québec (Blais 1983; Morin et al. 1993; Jardon et al. 2003; Bouchard et al. 2006) and five conducted in other parts of the province (Blais 1961, 1965; Morin and Laprise 1990; Krause 1997; Boulanger and Arseneault 2004). While none of the studies in western Québec detected an outbreak between 1881 and 1899, outbreaks detected in three studies in other parts of the province attributed growth reductions in host trees from about 1870-1883 to budworm outbreaks. Because outbreaks in other parts of Québec started about 10 years earlier, we considered the possibility that the outbreak we detected from 1881-1889 was an artifact of the procedure used to remove the climate signal from host tree-ring chronologies. This would occur if the non-host was more sensitive, and had more positive growth responses, to climate variations than the host. However, analyses of growth-climate relationships (Pearson correlations and response function analyses) indicated otherwise. While the 1851-1867 outbreak we detected was in close synchrony to a 1850-1860 outbreak detected by Jardon et al. (2003), no other studies attributed growth reductions to an outbreak around this time. The outbreak we detected between 1823 and 1838 occurred in close synchrony with outbreaks detected in all other studies over Québec except one (Blais 1981). We thought that the outbreak we detected from 1801-1813 might be an artifact of a small sample size, but all other studies in Quebec except two (Blais 1981; Morin and Laprise 1990), attributed growth reductions around this time to a budworm outbreak. The two most recent outbreak reconstructions in Québec (Jardon et al. 2003; Boulanger and Arseneault 2004) report strong periodic tendencies in the occurrence of budworm outbreaks and given outbreak return-intervals

between 29 and 42 years, all the outbreaks we detected prior to 1900 would fit with such a cyclical outbreak.

2.7.2 Budworm outbreak dynamics and bioclimatic variability

With outbreaks occurring about every 29 years, the results of this study do not support the notion that budworm outbreaks have become more frequent in Québec over the last two centuries (Blais 1983; Morin et al. 1993). Similar conclusions were reached regarding budworm outbreaks in other parts of North America (Royama 1984; Parish and Antos 2002; Jardon et al. 2003; Ryerson et al. 2003). Moreover, the duration, severity (% trees affected over the study area) and the extent of outbreaks also did not increase over the last two centuries in our study area. While budworm outbreaks occurred periodically, outbreak duration, severity and extent varied in a non-linear fashion over time. These findings suggest that budworm outbreak dynamics not only relate to intrinsic budworm population processes (Royama 1984) but probably also to external bioclimatic factors that have indirect influences on budworm populations at local and regional scales.

The fact that all budworm outbreaks in our study area occurred during positive phases of December NAO, when winters were on average warmer, suggests winter temperatures could have an influence on both the duration and severity of budworm outbreaks. This hypothesis is supported by Candau and Fleming (2005) who report that budworm-caused defoliation were less severe when minimum winter temperatures dropped below -23.3°C . Instrumental weather data for our study area (Environment Canada 2002) show that temperatures in December are strongly correlated with temperatures during other winter months (January and February). While mean minimum temperatures below -23.3°C were uncommon in December, they frequently occurred in January and February. In fact, minimum January temperatures below -30°C , in 1935 and 1945, marked the end of the 1920s and the 1940s outbreaks, providing convincing evidence that winter temperatures can affect outbreak duration and severity.

However, years with cold winters also had cold springs – mean minimum May temperatures below zero occurred in 1935, 1936 and again in 1945 (Environment Canada 2002). This increases the probability that late spring frosts will kill newly flushed foliage and the larvae feeding on it (Cerezke and Volney 1995). Unusually low temperatures might also generate phenological asynchrony between budworm and its hosts reducing the probability of outbreaks in some years. The physiological mechanisms underlying herbivore and plant phenology are affected by environmental cues like temperature, but not necessarily in the same way (van Asch and Visser 2007).

The long debated ‘climate release’ hypothesis proposes that a series of unusually dry summers initiate spruce budworm outbreaks because drought stress decreases host resistance to defoliation and increases prime budworm overwintering sites (i.e., host pollen cones) (Greenbank 1963; Mattson and Haack 1987; Ayres 1993). The fact that we found outbreaks occurring squarely during wet periods refutes this hypothesis. But, our results are consistent with the findings Swetnam and Lynch (1993); western spruce budworm outbreaks in the San Juan mountains of Colorado occurred years when summers were wetter than normal. They suggested that a greater quantity and quality of host foliage during wet periods may explain the occurrence of budworm outbreaks.

In 1983, Blais proposed that the more severe budworm outbreaks observed in the 20th century could be attributed to an increase in the abundance of *A. balsamea* caused by fire suppression, silviculture, and insecticide spraying to protect hosts for budworm outbreaks. Although *A. balsamea* increased over time within all the stands we sampled, no concomitant linear increase in outbreak severity or extent was observed among these stands. However, stand host abundance alone is unlikely to explain variations in budworm outbreak dynamics. Host vulnerability, as a function of tree size or age, also plays a role with small, younger *A. balsamea* being less vulnerable than large, mature trees (Bergeron et al. 1995; MacLean 1980). These size/age variation in vulnerability occur because *A. balsamea* produce proportionately less new foliage every year as they age and become increasingly larger (Waring 1987). In our study area, two major episodes of *A. balsamea* recruitment and tree occurred from the time stands established

following fire to the time they formed mature stands. This means that most *A. balsamea* were greater than > 60 years old (i.e., a largely even-aged stand) from about 1890-1910, around 1942 and from about 1985-1994, corresponding to the approximate times periods of the last 3 budworm outbreaks.

A reduction in *A. balsamea* over landscapes may explain why outbreaks were less extensive (i.e., occurred in fewer stands) during the last two outbreak periods (1937-1945 and 1972-1987) than during the 1923-1934 outbreak. Between 1900 and 1920, the stands we sampled were part of large expanses of late-successional forest in which mature *A. balsamea* were more abundant than any other tree species (Bergeron 2000). In 1923 and 1944, extensive fires converted a significant portion of this landscape to deciduous forests (Dansereau and Bergeron 1993). Other studies in Quebec have shown an increase in deciduous species in forests is related to a decrease in outbreak severity and that a greater abundance and diversity of budworm natural enemies in these forests (Cappuccino et al. 1998; Quayle et al. 2003).

2.8 Conclusions

After removing effects of climate on radial growth of *A. balsamea* and *P. glauca*, budworm outbreaks were inferred from several prolonged periods of reduced over the last 200 years. These outbreaks conformed to documentary archives of budworm outbreaks and were in synchrony with outbreaks detected in other dendrochronological studies. Outbreak occurred periodically over the last 200 years with a mean outbreak return-interval of about 29 years (range: 14 and 42 years). The severity (% trees affected over all stands) or extent (% stands affected) of outbreaks did not increase over the last century but some outbreaks were more severe and extensive than others, and fluctuating bioclimatic conditions play a role in generating outbreak patterns. The most severe outbreak occurred when wet summers and warm winter (or spring) temperatures were coincident with abundant mature *A. balsamea*. These findings are consistent with other recent landscape-level analyses of budworm outbreak patterns (Candau and

Fleming 2005) and suggest a suite of biological mechanisms control budworm population dynamics and the impact of this defoliator on forests: the direct effects of climate on budworm survival, host vulnerability to defoliation (e.g., phenological synchrony of host and budworm, foliage quality and abundance, tree size/age) and natural enemy abundance.

While much of the boreal zone is expected to get drier, boreal forests in the eastern part of Canada may get moister, reducing wildfire frequency (Flannigan et al. 2001). In the absence of fire, mature *A. balsamea* forests could become more abundant in boreal landscapes of the future. Given outbreaks in our study area were most severe when summers were moister and winters were warmer than average, global climate change could lead to more severe future budworm outbreaks in the absence of forest management interventions.

2.9 Acknowledgements

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Lien: L'article précédent a suggéré que la composition de la mosaïque forestière environnant influence la sévérité des épidémies dans les peuplements dominé par le sapin baumier. Dans l'article suivant, nous avons testé cette hypothèse.

3 ARTICLE II - LOCAL STAND CHARACTERISTICS AND LANDSCAPE CONTEXT INFLUENCE THE SEVERITY OF SPRUCE BUDWORM OUTBREAKS IN BOREAL FORESTS OF QUEBEC

(Manuscrit en préparation à Ecological Applications)

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3.1 Résumé

Vingt-sept peuplements dominés par *Abies balsamea* [L.] Mill. ont été échantillonnés pour déterminer l'influence des caractéristiques des peuplements et de la structure du paysage environnant (aux échelles spatiales différentes) sur la sévérité des diminutions de croissance radiale à la cause des épidémies de la tordeuse des bourgeons de l'épinette dans la forêt boréale du nord-ouest du Québec. Des échantillons (carottes et disques) ont été recueillis de mature *Abies balsamea* dans chaque peuplement et en utilisant les techniques dendrochronologiques, des chronologies moyennes de croissance radiale ont été construites. Ces chronologies ont permis de caractériser la croissance des peuplements pendant la dernière épidémie de la tordeuse (1971-1985). En utilisant une analyse de groupement, les peuplements ont été classifiés en trois groupes représentant les épidémies légères, modérés et sévères, avec des diminutions de croissance moyennes de 21%, de 43%, et de 60%, respectivement. La moyenne maximale de réduction de croissance parmi des peuplements touchés sévèrement était de 85%. L'analyse de redondance a indiqué que les caractéristiques des peuplements et le pourcentage des peuplements feuillus dans la mosaïque forestière expliqueraient des proportions significatives de la variation dans la sévérité des diminutions de croissance sur *Abies balsamea*. Les épidémies furent plus sévères dans les peuplements où les hôtes ont été abondantes et dans les paysages où le pourcentage des peuplements feuillus a été plus bas. L'effet de la composition de la mosaïque forestière était plus important à l'échelle spatiale de 1000 m. Les résultats de cette étude soulignent la nécessité de considérer la composition du paysage environnant pour évaluer leur vulnérabilité aux épidémies de la tordeuse des bourgeons de l'épinette.

Mots-clés: sapin baumier, forêt boréale, dendroécologie, perturbation, processus écologique et patrons de végétation, structure des forêts, composition du paysage, épidémies de la tordeuse des bourgeons de l'épinette, composition du peuplement

3.2 Abstract

Twenty-seven *Abies balsamea*-dominated stands were sampled to examine the influence of local stand characteristics and surrounding landscape structure, at different spatial scales, on the duration and intensity of *A. balsamea* growth reductions caused by spruce budworm outbreaks in boreal forests of northwestern Quebec. Increment cores and basal discs were collected from mature *A. balsamea* in each stand, and dendroecological techniques were used to develop mean standardized chronologies of tree-ring width. Chronologies were used to examine stand growth responses during the last spruce budworm outbreak (1971-1985). Using factor analysis, stands were classified into three groups representing light, moderate, and severe spruce budworm outbreaks that had 21, 43, and 60% mean radial growth reductions, respectively. Mean maximum growth reduction among stands with severe outbreaks was 85%. Redundancy analysis indicated that local stand characteristics and the percentage of deciduous-dominated forests in surrounding forest landscapes explained a significant proportion of the variance in *A. balsamea* growth responses to budworm outbreaks. Outbreaks were most severe where host trees were abundant and where the percentage of deciduous-dominated forests in surrounding landscapes was low. The effect of landscape context was most influential at a spatial scale of 1000 m. This study emphasizes the need to consider composition of surrounding landscapes when evaluating stand vulnerability to spruce budworm outbreaks.

Keywords: balsam fir, boreal forest, dendroecology, disturbance, ecological process and vegetation pattern, landscape composition, spruce budworm, stand composition

3.3 Introduction

The ecological processes occurring in a particular patch of forest are strongly influenced by local site and stand characteristics. However, ecologists are increasingly aware that most local ecosystem functions are influenced at spatial scales much larger than a single patch of forest. A growing number of studies demonstrate that local ecological processes are also affected by the larger-scale forest patterns and processes of surrounding landscapes. For example, community assembly and patterns of succession following forest disturbance may vary substantially depending upon the tree species composition of the surrounding forest landscape (Frelich *et al.* 1998; Metzger 2000; Campbell and Antos 2003). Similarly, the probability and intensity of forest disturbances themselves may be dependant on characteristics of surrounding landscapes (Niklasson and Granstrom 2000; Frelich and Reich 2004). Given that structure and composition of forest landscapes are rapidly changing due to intensive land-use activities and global climate change (Overpeck *et al.* 1991; Goldewijk and Ramankutty 2004), it is becoming increasingly important to understand how local ecological processes in a particular patch of forest are linked to the larger-scale patterns and ecosystem processes of surrounding landscapes. Incorporation of this information into forest management strategies will improve our chances of conserving the ecological integrity of future forest ecosystems and thus their ability to provide benefits to society in perpetuity.

Periodic spruce budworm (*Choristoneura fumiferana* Clem.) (Lepidoptera: Tortricidae) outbreaks are natural disturbances of North American boreal and mixedwood forests. Spruce budworm larvae feed preferentially on the youngest available foliage of *A. balsamea* and *Picea* spp., and during population outbreaks repeated annual defoliation can substantially reduce growth and cause death of host trees (Bergeron *et al.* 1995). Because of their ability to cause tree deaths, budworm outbreaks are important ecological processes that play a key role in restructuring forests to drive stand dynamics, promote nutrient cycling and maintain biological diversity (Franklin *et*

al. 1987).

Localized spruce budworm outbreaks have occurred in *Abies balsamea*/*Picea* spp.-dominated forests for millennia (Simard *et al.* 2006) and their ecological role remains unchanged through history. However, several researchers proposed that budworm outbreaks have become progressively more severe over the last century (Blais 1983; Morin *et al.* 1993; Boulanger and Arseneault 2004). Having reduced annual timber supplies by up to 22%, the last outbreak in eastern Canada had the most substantial socioeconomic impacts on record (Sterner and Davidson 1982; Power 1991; National Forestry Database 1995). It has been proposed that changes in forest composition, due to intensive human land-use activities and global climate change, account for this trend towards more severe outbreaks. In eastern Canada, logging, fire suppression, silvicultural practices and insecticide spraying can increase the abundance of *A. balsamea*- and *Picea* spp.-dominated forests in landscapes, causing a shift from fine-grained forest mosaics of varying stand types to coarser-grained forest landscapes composed of contiguous, host-dominated stands. Increasingly moister climates resulting from global climate change seem to be decreasing fire frequency in eastern North America (Bergeron and Leduc 1998) and having the same end effect i.e., more host-dominated forests in landscapes.

The objective of this research was to test the hypothesis that surrounding forest landscape composition influences the severity of spruce budworm outbreaks in *A. balsamea*/*Picea glauca*-dominated stands. By severity we mean the impact of budworm outbreaks on host growth. A number of studies on herbivore population levels and host defoliation levels suggest that surrounding landscape composition could have an important influence on the severity of forest insect outbreaks in stands (Roland 1993; Kouki *et al.* 1997; Roland and Taylor 1997; Radeloff *et al.* 2000; MacKinnon and MacLean 2003). Only three studies have directly attempted to examine the impact of landscape composition on the severity of budworm outbreaks. Two studies focused on host mortality levels (Bergeron *et al.* 1995; Cappuccino *et al.* 1998) and another on growth in mixedwood forests of New Brunswick (MacKinnon and MacLean 2004). In

this study, we used a dendroecological approach to describe how tree growth patterns associated with spruce budworm outbreaks (i.e., the duration and intensity of growth reductions) varied among stands surrounded by compositionally different boreal forest landscapes in northwestern Quebec. However, detecting a relationship between surrounding landscape patterns on local ecological processes may be highly dependant on the spatial scale of analysis (Roland and Taylor 1997; Metzger 2000; Thies *et al.* 2003). As such, we evaluated the influence of surrounding landscape composition at two spatial scales, namely in circular landscape neighbourhoods having radii of 500 m and 1000 m. The relative influence of local stand characteristics and surrounding landscape composition on the severity of budworm outbreaks in stands was also examined.

3.4 Methods

3.4.1 Study area

This study took place in the southeastern portion of the Canadian boreal forest near the Quebec-Ontario border (48°30'N, 79°25'W) (Fig. 3.1). The landscape alternates between rolling hills with moraine deposits and lowlands covered by clays from the post-glacial lakes (Vincent and Hardy 1977). The climate is continental with a mean annual temperature of 0.6 ° C, mean annual precipitation of 822.7 mm, and a mean annual frost-free period of 64 days, although freezing temperatures can occur at any time throughout the year (Environment Canada 2002).

Forested landscapes in the region are complex mosaics of stands whose composition is determined primarily by surficial deposits and time since fire disturbance (Bergeron 2000). On mesic sites of clay deposits, early successional stands are dominated by *Populus tremuloides* Michx., mid-successional stands by *A. balsamea*, *Betula papyrifera* Marsh., *Picea glauca* (Moench) Voss, and *P. mariana*, and late-successional stands by *A. balsamea* and *Thuja occidentalis* L., with a lesser component of *P. glauca*. On drier

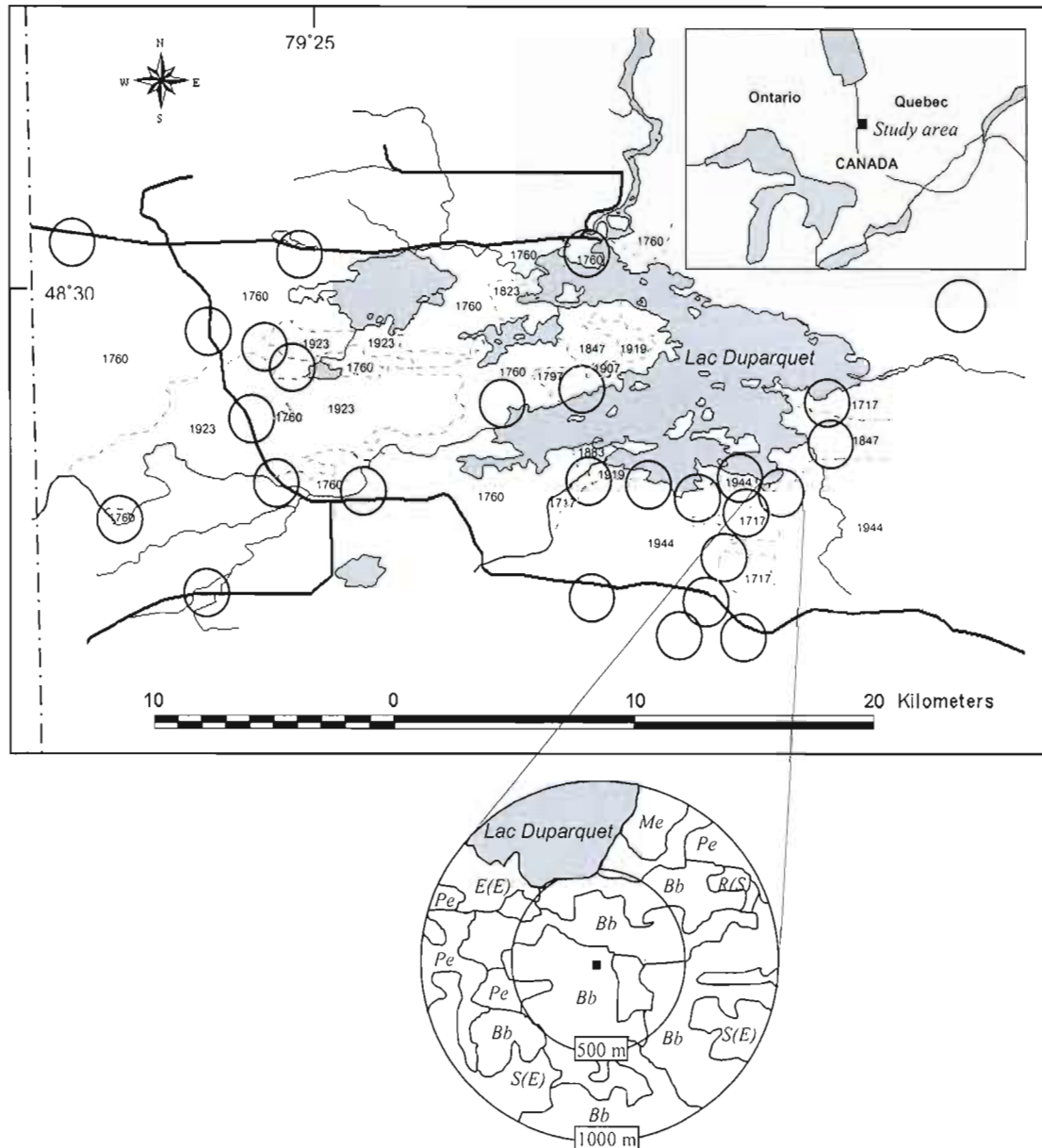


Figure 3.1. Map of the study area. (a) Location of the landscape neighbourhoods (the circles of 1 km radii) surrounding 27 of the *A. balsamea*/*Picea* spp.-dominated stands sampled. (b) An example of the deciduous-dominated landscape neighbourhood surrounding a 0.32 ha patch of *A. balsamea*/*Picea* spp. forest sampled. Labels in each forest polygon indicate the dominant tree species (Bb=*Betula papyrifera*, Pe=*Populus tremuloides*, S=*Abies balsamea*, E=*Picea glauca*, Me=*Larix laricina*, R=conifer species).

sites of moraine deposits, *B. papyrifera* dominates early successional stands. Mid-successional and late-successional stands are dominated by the same species that occur on clay deposits but these drier sites usually have more *P. mariana* than *P. glauca*. Early and mid-successional stands on bedrock are dominated by *P. mariana* and *Pinus banksiana* Lamb. or *P. resinosa* Ait. with *T. occidentalis* becoming more abundant as stands age. Bogs and other hydric sites are dominated by *P. mariana*, *T. occidentalis*, and *Larix laricina* (Du Roi) K. Koch. *Fraxinus nigra* Marsh. dominates floodplains.

Fire has occurred throughout the area, with the most recent stand-replacing fires occurring in 1923 and 1944, and the oldest records of fires in 1717 and 1760 (Dansereau and Bergeron 1993). The last spruce budworm outbreak in this region occurred from 1971-1985 (Ressources naturelles Québec, *unpublished aerial survey data*). Human land-use activities include forestry, mining and farming but they are restricted to the northern part of the study area, which is more populated.

3.4.2 Study design and stand sampling

Québec ecoforestry maps (1:20 000), which delineate individual forest polygons (i.e., stands) and assign them a unique set of attributes including a stand identifier, species composition, species percentages, crown closure, height class, maturity class, and soil drainage class, as well as aerial photographs, were used to identify *A. balsamea*/*P. glauca*-dominated forests in our study area. All stands were grouped into three broad categories based on surrounding landscape composition, which is highly influenced by fire history (Dansereau and Bergeron 1993): 1 – *deciduous landscapes* were disturbed by fire less than 100 years ago and were covered largely (>75%) by deciduous-dominated stands in which paper birch or trembling aspen were the dominant species; 2 – *coniferous landscapes* have remained largely undisturbed by fire for more than 200 years and were covered mostly by fir/spruce-dominated stands; and 3 – *mixed landscapes* had less extensive recent fires than deciduous landscapes and thus 25-75% of the landscape was covered by deciduous-dominated stands. A subset of 27 stands,

evenly distributed among the above landscape categories and located at least 1 km apart, were sampled. Stands were prioritized for sampling based on their proximity to roads, or the shore of Lac Duparquet.

Within each patch of *A. balsamea*/*Picea glauca* forest, a 20 x 20 m plot, located at the centroid of the stand, was used to measure and quantify local stand characteristics. Slope (%), elevation (m), topographic position (lower, mid-, and upper slope), and ground surface shape (straight, convex, concave) were recorded. Soil characteristics (e.g., thickness and texture of humus and mineral soil layers, coarse fragment content) were measured in a soil pit dug at the center of each plot. The breast height (1.3 m) diameter of all trees species was tallied by 5 cm classes. The percent crown cover of all shrubs and herbaceous species in the plot was estimated visually over the entire plot, and in 5 x 5 m subplots when the understory vegetation was particularly dense. Data on site, soils, and indicator plant groups were used to assign stands to soil nutrient and moisture classes, which are described by Bergeron and Bouchard (1983) and Brais and Camiré (1992), respectively. This information permitted us to evaluate the potential effects of site differences on *A. balsamea* growth patterns.

Tree-ring data obtained from increment cores and basal disks were used to characterize the severity of growth reductions caused by defoliation during the last spruce budworm outbreak and to determine host ages. In each stand, two increment cores were extracted from opposite sides and at the base of 10-15 trees. The largest, and presumably oldest, *A. balsamea* and *P. glauca* closest to the plot centre were sampled. Up to fifteen basal disks were collected from dead *A. balsamea*; the number of samples collected from dead trees reflected the percentage of budworm-caused tree death in stands.

3.4.3 Constructing chronologies of radial growth

All *A. balsamea* increment cores and basal disks were prepared in the laboratory following standard dendrochronology procedures (Swetnam *et al.* 1985). After sanding and mounting of cores, tree rings were visually cross-dated within plots, using a modified skeleton plot method (Yamaguchi 1991) and measured to the nearest 0.001 mm using a Velmex™ Uni Slide Micrometer connected to a computer. The program COFECHA (Holmes 1983) was used to verify dating. Tree-ring series that did not cross-date well with other samples in the stand (i.e., $r < 0.350$) were checked for dating or measurement errors and corrected as necessary. Series that remained poorly correlated with other samples were then eliminated from the dataset of each stand. On average, 11% of the series were removed. A sample size of at least 10 *A. balsamea* trees remained in the dataset for all stands except two, which had eight and nine trees.

Using the computer program ARSTAN (Cook 1985), series of raw tree ringwidths (mm) for each stand were standardized following methods outlined by Krause and Morin (1999). The resulting dimensionless index values were averaged over all tree-ring series in a stand to produce a standardized master (i.e., mean) tree-ring chronology for each stand. Ringwidth index values of 1.0 are equivalent to mean tree growth in a stand, values >1.0 represent above-average growth and values <1.0 indicate growth reductions.

3.4.4 Quantifying landscape context

Landscape neighbourhoods – the area within a 500 m and 1000 m radius of the centroid of sampled *A. balsamea*/*Picea glauca* stands – were delineated on ecoforestry maps derived from 1983 aerial photography of the study area. The forest polygons within each landscape neighbourhood were digitized and attributes describing each polygon were entered into a database. Mapped polygons extending beyond the landscape neighbourhood were considered to end at the edge of the circle delineating the landscape neighbourhood. ArcView GIS was used to calculate a set of variables

characterising landscape neighbourhoods. The areas covered (%) by *A. balsamea*-dominated forests, host-dominated forests (both *A. balsamea* and *Picea* spp.-dominated forests), non-host conifer dominated forests, and deciduous-dominated forests were calculated. The compositional complexity of landscape neighbourhoods, measuring the relative amounts of deciduous-dominated and coniferous-dominated forests, was calculated using the Shannon index of diversity (Shannon and Weaver 1949). The area of host-dominated forest contiguous with the *A. balsamea*/*Picea* spp. stand sampled was also calculated.

3.4.5 Data analysis

Cluster analysis techniques, similar to those employed in other studies examining spatial patterns in insect outbreak population dynamics and temporal variability of impacts on forests (Williams and Liebhold 2000; Aukema *et al.* 2006) were used to extract and identify similar *A. balsamea* annual radial growth responses to the last spruce budworm outbreak in our study area. Hierarchical agglomerative clustering techniques, which use a sorting algorithm (i.e., linkage method) to first group similar entities and then successively merge them into similar groups producing a dendrogram, were used to cluster radial growth patterns (spanning 1970 to 1995) from 27 stands into k similar groups. A variety of linkage methods can be used (Legendre and Legendre 1998). We overlaid results of various linkage methods onto constrained ordinations of radial growth patterns (see below) and found that all methods yielded similar conclusions regarding relationships between outbreak severity (i.e., growth reduction) and these explanatory variables. Thus, we only report the results obtained through the unweighted pair-group method with arithmetic mean (UPGMA) linkage method. Choosing the most appropriate number of k clusters in which to group radial growth patterns was guided by a non-hierarchical clustering method: principal components analysis. The optimal number of clusters was chosen based on the Kaiser criterion whereby the number of principal components having an eigenvalue greater than 1

indicates the number of clusters in which to group radial growth patterns (Legendre and Legendre 1998). The chronologies deemed similar through clustering techniques were averaged together and statistics summarizing intensity and duration of growth reductions for each chronology cluster were used to classify severity of budworm outbreaks among the 27 stands sampled.

Redundancy analysis (RDA) was used to explore relationships between *A. balsamea* radial growth patterns and forest composition. RDA is a constrained ordination method that combines multiple regression and principal components analysis to model linear relationships between multivariate response data (Y) and a set of explanatory variables (X) (Rao 1973). The program CANOCO (v.4.5, ter Braak and Šmilauer 2002) was used to conduct RDAs on a matrix of response variables comprised of *A. balsamea* tree-ring width indices for each stand from 1971-1995. Matrices of explanatory variables described: i) local stand characteristics, and ii) forest composition of landscape neighbourhoods. Because of substantial correlation among explanatory variables, a stepwise forward selection procedure was used to determine which subset of stand and landscape variables had the greatest influence on the variability in *A. balsamea* radial growth patterns among stands. Variables were entered into the model if *p*-values of partial Monte Carlo permutation tests were <0.10 . A Monte Carlo permutation test was also used to evaluate significance of the final model, with the null hypothesis being that variation in *A. balsamea* growth patterns among stands was random, and not influenced by explanatory variables included in the model. Explanatory variables were transformed to improve normality – arcsine transformations were used on proportional variables (e.g., percentage of deciduous forests in landscapes) and log transformations were used on others (e.g., average *A. balsamea* age, soil drainage index). To determine the maximum potential variance explained by each variable entered into the model, RDAs were then run separately for each variable.

3.5 Results

3.5.1 Local stand characteristics and surrounding landscape composition

Our goal was to select stands with a composition of >75% spruce-fir. However, basal area calculations from stand measurements indicated somewhat more variation in stand composition than Québec ecoforestry maps indicated (Table 3.1). *A. balsamea*-*P. glauca* content was >75% in 13 stands sampled and >50% in 10 others. The remaining six stands had <50% spruce-fir content but the highest proportion of non-host conifers – mainly *T. occidentalis*, a characteristic species of late-successional stands. All stands were composed of greater than 55% conifer species. Nine stands had between 26 and 41% deciduous, *B. papyrifera* being the dominant species in all but two of these stands, which had more *P. tremuloides*.

While sampled stands varied somewhat with respect to soil moisture and nutrient regimes (Table 3.1), variation in stand tree species composition was not significantly correlated ($p=0.17$ to 0.96) with this edaphic gradient. However, stand tree species composition was significantly correlated with the mean age of canopy-dominant budworm hosts – while the mean age of *A. balsamea* was positively correlated with the abundance of non-host conifers ($p=0.08$) and negatively correlated ($p=0.05$) with the percentage of all hosts, the mean age of *P. glauca* was positively correlated with the percentage of deciduous in stands. These results suggest a gradient in stand tree species composition that is associated with stand age, whereby the youngest stands we sampled were mature forests comprised predominantly of *A. balsamea* and *P. glauca* and the oldest stands had more non-host conifers (mainly *T. occidentalis*) and deciduous (mainly *B. papyrifera*). Due to greater than expected variation in local stand conditions, stand characteristics were included as covariables in further analyses that also tested the forest composition effects of surrounding landscapes.

By design, the composition of forest landscapes within 1000m and 500m of stands varied substantially, with all landscape variables (except nonhost-dominated forests)

Table 3.1. Local stand characteristics and forest compositional characteristics landscape neighbourhoods surrounding 27 *A. balsamea*/*Picea* spp.-dominated forest patches sampled in northwestern Quebec.

Variable	Description	Average	Std dev.	Min.	Max.
<u>Local stand characteristics</u>					
Tree species composition ^a :					
AB-S	% <i>Abies balsamea</i>	44	25	8	100
HOST-S	% <i>A. balsamea</i> and <i>P. glauca</i>	70	23	18	100
NONHOST-S	% non-host conifers	10	28	0	75
TDEC-S	% deciduous species	20	13	0	41
Edaphic conditions:					
SOILMOIST ^b	Soil moisture regime	3.6	0.87	2	5
RNR ^c	Relative soil nutrient regime	2	0.5	1	3
Mean ages of dominant host trees:					
AB-AGE ^d	<i>A. balsamea</i>	63	8	42	76
SW-AGE2	<i>P. glauca</i>	85	27	47	168
<u>Composition of landscape neighbourhoods</u>					
Within 1000m of sampled patch:					
AB-1000	% <i>A. balsamea</i> -dominated forests	33	24	0	78
HOST-1000	% <i>A. balsamea</i> and <i>P. glauca</i> -dominated forests	49	26	2	95
NHOST-1000	% non-host coniferous-dominated forests	6	11	0	47
TDEC-1000	% forest dominated by deciduous species	42	23	3	83
DIV-1000	Shannon index of diversity, measuring relative amounts of deciduous-dominated and conifer-dominated forests	0.56	0.2	0.15	0.69
ABCONT-1000	Area (ha) of <i>A. balsamea</i> -dominated forests contiguous with sampled patch	48	51	0.04	157
HCONT-1000	Area (ha) of host-dominated forest contiguous with sampled patch				
Within 500m of sampled patch:					
AB-500	% <i>A. balsamea</i> -dominated forests	39	30	0	91

Table 4.2 (cont.)

HOST-500	% <i>A. balsamea</i> and <i>P. glauca</i> -dominated forests	56	30	0	100
NHOST-500	% non-host coniferous-dominated forests	3	7	0	29
TDEC-500	% forest dominated by deciduous species	38	29	0	92
DIV-500	Shannon index of diversity, measuring relative amounts of deciduous-dominated and conifer-dominated forests	0.47	0.20	0.06	0.69

^a tree basal area (m²/ha) as percentage of total tree basal area. Dominant trees are >15cm dbh. Includes living and dead trees at the time of sampling. ^b Soil moisture classes are: 2=moderately dry, 3=fresh, 4=moist, 5=very moist ^cRelative soil nutrient regime classes are 1= submesotrophic, 2=mesotrophic, 3=slightly eutrophic. ^d Ages of the largest, presumably oldest trees. Because cores were taken at about 30 cm above the point of germination and because some old trees had rotten centers, these data represent minimum ages.

generating a compositional gradient from nearly 0 to 100% (Table 3.1). Local stand characteristics were not correlated with any of the variables describing surrounding landscape composition ($p > 0.10$). However, there was a high degree of correlation among variables describing landscape composition within each of the spatial scales tested (i.e., landscape neighbourhoods of 1000m and 500m; $p < 0.001$ to 0.03). In addition, each variable describing surrounding forest landscape was significantly correlated across the two spatial scales sampled ($r = 0.80$ to 0.85 $p < 0.001$) and because of this, further analyses focused only on exploring relationships between *A. balsamea* growth patterns and the characteristics of landscapes within 1000m of sampled stands.

3.5.2 Variability in *A. balsamea* growth responses to budworm outbreaks

Following principal components analysis of *A. balsamea* radial growth patterns, the eigenvalue for each principal component was illustrated in a “scree plot”. The first three principal components had eigenvalues greater than one and accounted for greater than 90% of the variation in radial growth patterns among stands. Based on these results, and the dendrogram produced by UPGMA agglomerative clustering techniques (Fig. 3.2), *A. balsamea* radial growth chronologies from 27 stands were grouped into three clusters of similar radial growth patterns. Individual stand chronologies of radial growth within each cluster were averaged to produce three cluster chronologies of radial growth: Cluster 1, Cluster 2 and Cluster 3 (Fig. 3.3). These three *A. balsamea* chronologies differed mainly in their patterns of radial growth from 1979 onwards (Fig. 3.3). Substantial reductions, which began between 1980 and 1981, occurred amongst all clustered radial growth patterns. Cluster 1 chronologies had the shortest period of reduced growth, with maximum growth reductions not exceeding 34% (Table 3.2).

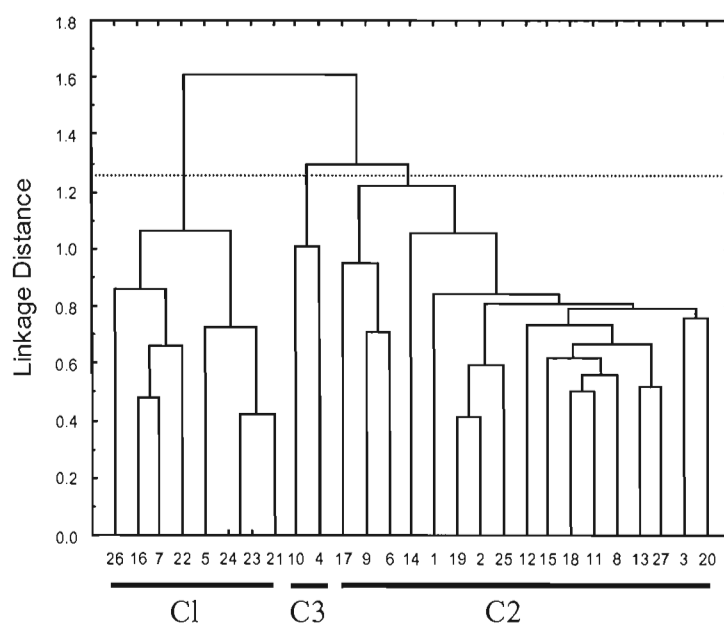


Figure 3.2. Dendrogram resulting from hierarchical cluster analysis of *Abies balsamea* annual radial growth responses to the last spruce budworm outbreak in northwestern Quebec. The dendrogram uses the weighted pair-group with arithmetic mean linkage method (UPGMA) with Euclidean distances. The horizontal dotted line represents the number of clusters that describe 90% of the variation in radial growth patterns among stands. C1, C2, and C3 (solid black lines) show how many stands (numbered 1 to 27) occur in each cluster.

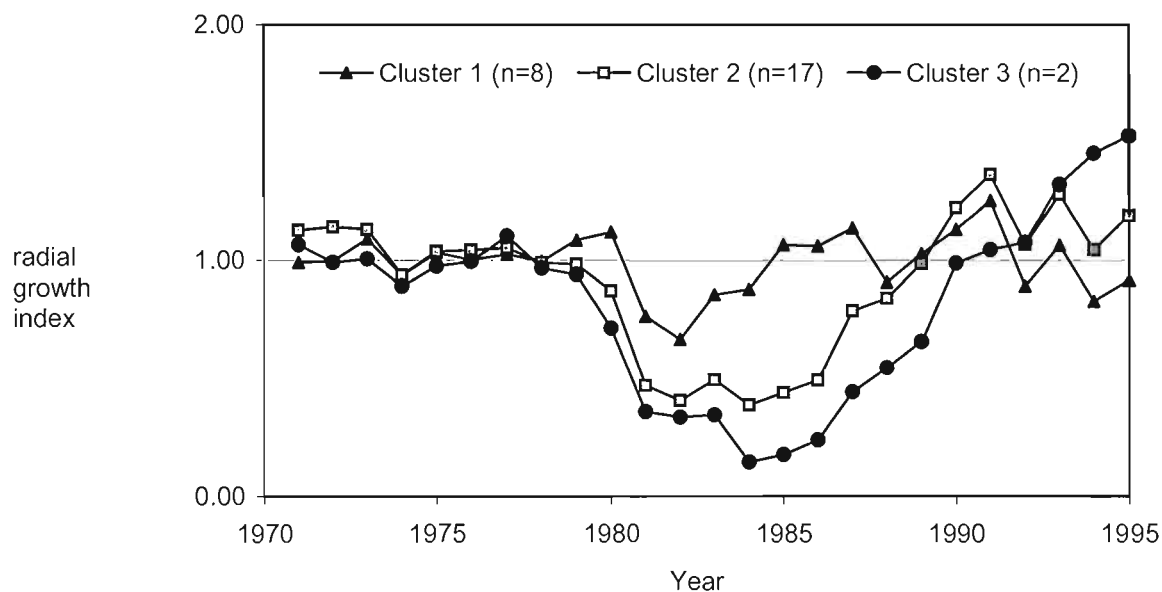


Figure 3.3. *A. balsamea* radial growth responses to a spruce budworm outbreak between 1971 and 1985 in northwestern Quebec. Radial growth indices were average within each of the stand groupings identified through cluster analysis. Radial growth indices of 1.0 represent average tree growth; indices >1.0 indicate above average radial growth and indices <1.0 indicate radial growth reductions.

Table 3.2. Characteristics of clustered *A. balsamea* radial growth chronologies and classification of spruce budworm outbreak severity for 27 spruce-fir dominated stands in northwest Québec.

	Cluster 1 chronology	Cluster 2 chronology	Cluster 3 chronology
No. stand chronologies	8	17	2
Duration of growth reduction *	4	9	10
Mean growth reduction (%)	21.0	43.4	60.0
Maximum growth reduction (%)	33.5	62.4	85.4
Year of maximum reduction	1982	1984	1984
First year return to average growth	1985	1989	1990
Outbreak severity class †	light	moderate	severe

* Number of years with growth reduced by at least 10%

†Based on the intensity and duration of growth reductions

3.5.3 Relationships between spatial variation in growth patterns and explanatory variables

Redundancy analysis (RDA) using a forward selection procedure indicated that two independent (i.e., largely uncorrelated) variables, percentage of hosts in stands (HOST-S) and percentage of deciduous forest within 1000m of the sampled stand (TDEC-1000), were significantly related to variation in *A. balsamea* growth patterns among stands (Monte Carlo permutation test $P=0.001$). Eigenvalues calculated through redundancy analysis on individual variables were used to determine maximum potential variance explained by each variable included in the model and the complementary landscape variable at the 500m spatial scale, TDEC-500 (Table 3.3). The percentage of total tree basal area occupied by budworm hosts (HOST-S) in a stand had the greatest influence on variation in *A. balsamea* growth patterns among the 27 stands sampled, with about 29% of the variation attributed to this variable. Landscape composition had the second most important influence, with about 13% of the variance in *A. balsamea* growth patterns being attributed to percentage of landscape neighbourhoods covered by deciduous-dominated forests (TEC-1000). At the 500m spatial scale, the percentage of a landscape neighbourhood covered by deciduous-dominated forests (TDEC-500) explained a smaller percentage of the variation (~8%).

Relationships between severity of budworm-caused growth reductions and local stand or surrounding landscape composition were illustrated by overlaying results of cluster analyses, which grouped common *A. balsamea* growth patterns into light, moderate, and severe outbreaks, onto an ordination diagram depicting results of RDA (Fig. 3.4). Stands with light outbreaks separated quite distinctly from those with moderate and severe outbreaks (Fig. 3.4), occurring predominantly in the upper right quadrant of the ordination diagram. While the total basal area occupied by hosts varied from average to above average in stands with light outbreaks, percentage of surrounding forest landscape covered by deciduous-dominated forests was less variable and among the highest of all stands sampled. Stands with moderate outbreaks occurred

Table 3.3. Percentage of the variation in *A. balsamea* radial growth patterns (1971-1995) among stands explained by: the percentage of hosts in stands (HOST-S), the percentage of surrounding landscape covered by deciduous forests within 1000 (TDEC-1000) and within 500 m (TDEC-500) among stands. *P*-values obtained through redundancy analysis are based on 999 unrestricted Monte Carlo permutations.

Explanatory variable	Maximum potential variance explained* (%)	<i>F</i> -ratio	<i>P</i>
HOST-S	28.6	10.03	0.001
TDEC-1000	13.3	3.83	0.020
TDEC-500	8.2	2.20	0.090

predominantly in the middle of the ordination plot and had below average to average percentage of deciduous forests in surrounding landscapes. The abundance of host species in stands was also below average to average. Two stands with severe outbreaks were located to the left of the ordination plot. While these stands had a below average to average percentage of deciduous forests in surrounding landscapes like moderate outbreaks, they were distinguished from most stands with moderate outbreaks because they had among the lowest percentage of hosts (Fig. 3.4).

3.6 Discussion

3.6.1 Influence of local stand characteristics on outbreak severity

Our results indicated a significant gradient in stand tree species composition that is probably related to stand age – stands with the youngest hosts, on average, were composed predominantly of *A. balsamea* and *P. glauca*, while stands with the oldest hosts had more non-host species like *T. occidentalis* and *B. papyrifera*. This apparent relationship between stand age and forest composition is consistent with general patterns of forest succession described for mesic sites in the eastern boreal zone (Bergeron 2000). Older stands have more abundant decaying wood that facilitates the establishment of *T. occidentalis* (Simard *et al.* 1998), and forest gaps generated by death of canopy dominant trees in old stands promotes regeneration of shade-intolerant *B. papyrifera* (Kneeshaw and Bergeron 1998; Bergeron 2000).

Variation in host abundance was the most important variable explaining differences in outbreak severity among stands. Stands with a greater percentage of hosts tended to have the least severe outbreaks. Given that previous studies have shown that outbreaks are more severe in stands dominated by hosts (Bergeron *et al.* 1995; Su *et al.* 1996), this was a somewhat surprising result. However, while all stands we sampled from were dominated by *A. balsamea* and *Picea* spp. (i.e., >55%), host abundance was highest

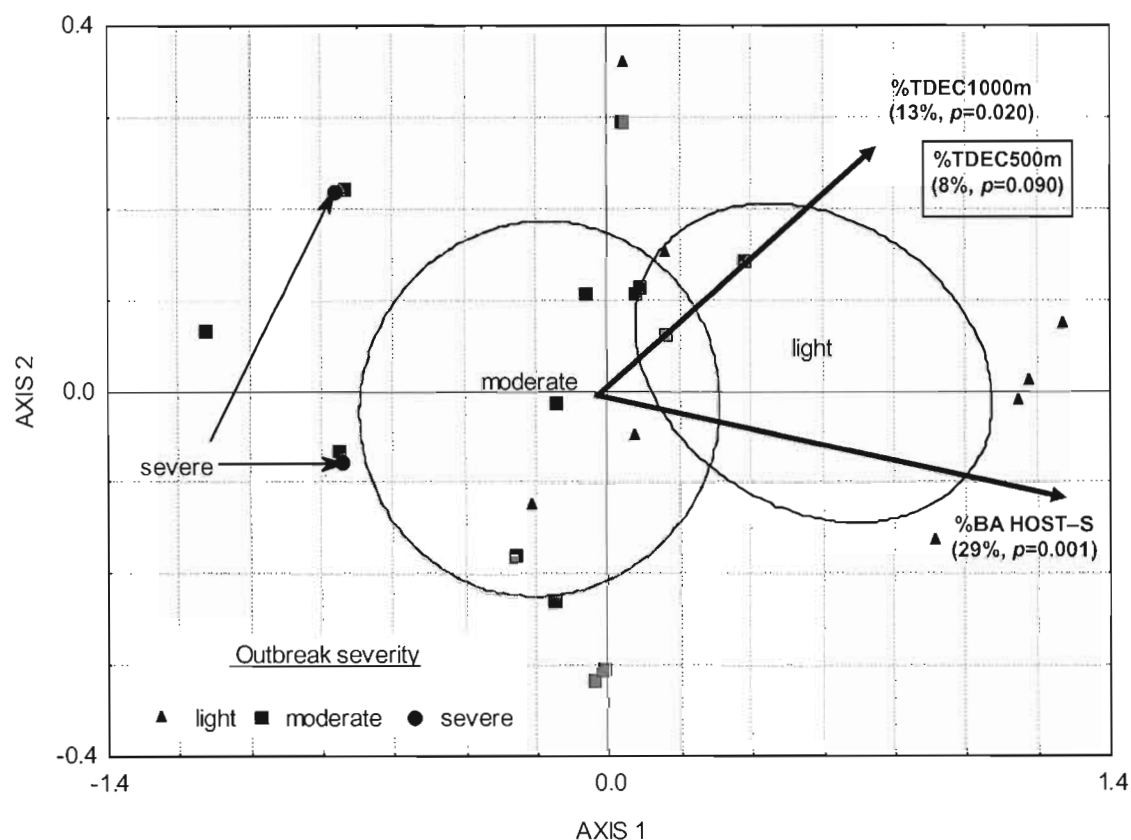


Figure 3.4. Redundancy analysis ordinating chronologies of *A. balsamea* growth in relation to the percentage of hosts in stands (HOST-S) and the percentage of deciduous-dominated forests covering landscapes within 1000m of stands (TDEC-1000). Stand dispersion is presented along the first 2 ordination axes as this captures 96% the relationship between the response and explanatory variables. The length and direction of eigenvectors (heavy arrows) indicate the relative influence of explanatory variables and the direction of the environmental gradient. The center of the diagram represents gradient mid-points. An overlay of growth pattern groupings obtained through cluster analysis illustrate relationships between light, moderate, or severe (light arrows) spruce budworm outbreaks and the explanatory variables. For each outbreak severity category, ellipses delineate the ordination space in which at least 67% of stands should occur. An ellipse could not be calculated for severe outbreaks due to a sample size of 2.

among the youngest stands. The *A. balsamea* in these young stands were probably much less vulnerable to the last budworm outbreak, generating the negative relationship between outbreak severity and host abundance we found in this study. This hypothesis is supported by intensive work in New Brunswick that examined relationships between *A. balsamea* vulnerability and tree and stand age (MacLean 1980). As trees age and become increasingly larger, they allocate more resources to maintenance tissues and produce proportionately less new foliage every year compared to younger trees (Waring 1987), making them more vulnerable to moderate defoliation levels. In addition, old trees that survive previous outbreaks are susceptible to root diseases (Ostaf 1983) and this stress may induce higher pollen cone production providing more abundant overwintering habitat for budworm larvae (Greenbank 1963). Moreover, while large trees are less abundant in old stands, the multi-layered canopies containing many younger hosts may help reduce dispersal losses during larval stages (Gustafson and Gardner 1996).

3.6.2 Influence of landscape context on outbreak severity

Our results support the hypothesis that surrounding forest composition influences severity of spruce budworm outbreaks in *A. balsamea*/*P. glauca*-dominated stands. This finding is consistent with several studies indicating the spatial context of stands can have an important influence on herbivore population and host defoliation levels (Roland 1993; Kouki *et al.* 1997; Roland and Taylor 1997; Radeloff *et al.* 2000; Thies *et al.* 2003; MacKinnon and MacLean 2004). In this study, the percentage of deciduous-dominated forests in surrounding landscapes was significantly negatively related to outbreak severity. Studies on the spatial patterns of budworm-caused *A. balsamea* deaths have produced analogous results — fewer hosts are killed when stands are located in deciduous-dominated landscapes (Bergeron *et al.* 1995; Cappuccino *et al.* 1998). Similarly, studies of host defoliation levels during outbreaks indicated that they were lower among stands with a high percentage of deciduous trees (Su *et al.* 1996). While

stand isolation from dispersing moths could be a contributing factor to lower outbreak severity in *A. balsamea*/*P. glauca* stands surrounded by deciduous landscapes, there is more evidence to indicate that a more diverse complex of budworm natural enemies in these stands has a substantial impact. In the same area where we conducted this study, Cappuccino *et al.* (1998) found that tachinid parasitoids of larvae, as well as ichneumonid parasitoids of pupae, caused higher budworm mortality in landscapes dominated by deciduous forests than in landscapes of extensive *A. balsamea*. Similarly, Quayle *et al.* (2003) found that parasitism of eggs by hymenoptera was greater in mixedwood stands than in those dominated by *A. balsamea*.

Among all the landscape composition variables we tested, the percentage of deciduous-dominated forests in surrounding landscapes had the most prominent influence on outbreak severity. However, percentage of deciduous-dominated stands was significantly negatively correlated with the abundance of host-dominated forests in landscape neighbourhoods and area of host forest contiguous with sampled stands, and positively correlated with diversity of landscape neighbourhoods. Thus, we cannot rule out the possibility that other aspects of surrounding landscape composition also influence outbreak severity. It is possible that two opposing aspects of landscape composition (e.g., the abundance of *A. balsamea*-dominated and the abundance of deciduous-dominated forests in landscape neighbourhoods) are acting in concert, but on different budworm population processes (i.e., fecundity, dispersal, parasitism), to affect the severity of budworm outbreaks observed in stands.

The percentage of deciduous-dominated forests within 1000 m of a stand explained more variance in the severity of a budworm outbreak than percentage of deciduous-dominated forests within 500 m of a stand. The spatial scale at which budworm-parasitoid interactions respond to landscape context may account for this difference. While we are not aware of any research that specifically examines this for spruce budworm parasitism, a couple of studies indicate that parasitism rates of other herbivorous insects respond to landscape context at various spatial scales. For example, Thies *et al.* (2003) tested the influence of agricultural landscape complexity on pollen

beetle (*Meligethes aeneus* F.) parasitism at eight spatial scales within circular landscape neighbourhoods ranging in diameter from 0.5 km to 3km. For each of the three ichneumonid parasitoids examined, they found that relationships between parasitism rates and landscape complexity were statistically significant at three spatial scales: 1, 1.5, and 2km. Roland and Taylor (1997) examined how parasitism rates of tent caterpillar (*Malacosoma disstria* Hubner) varied with landscape fragmentation at seven spatial scales (53 m to 3400 m) and found that each of the fly parasitoids examined responded to landscape structure at four of the seven spatial scales tested (53 to 850 m) that corresponded to their relative body sizes. Given information about the species that parasitize budworm in our study area (Cappuccino *et al.* 1998), and results of the above studies, we expect that the scale differences in relationships between forest composition and outbreak severity are due to differences in the scale that parasitoids respond to forest composition. An interesting extension of our study would be to test this hypothesis for spatial scales ranging from 50 m to 4000 m.

3.7 Conclusions

This study illustrated that forest composition at two spatial scales affect the severity of spruce budworm outbreaks in *A. balsamea*/*Picea glauca*-dominated stands of northwestern Quebec. However, host abundance in stands explained more variation in outbreak severity than the composition of surrounding forest landscapes, indicating local habitat characteristics had a stronger influence, indicating local habitat characteristics were more were a more important determinant of outbreak severity than the spatial context of stands. Nevertheless, stand context did have a significant independent effect on the severity of budworm outbreak in *A. balsamea*/*Picea glauca*-dominated stands, a finding that has important implications for managing forests to minimize socioeconomic impacts of future budworm outbreaks. Following the last spruce budworm outbreak, which caused as much as a 22% loss in annual timber harvest levels in Canada (Sternner and Davidson 1982; Power 1991; National Forestry Database 1995), the Canadian

Forest Service developed a decision support tool to project stand vulnerability to future spruce budworm outbreaks and evaluate management scenarios to minimize impacts. Currently, this tool relies on relationships between local stand characteristics and outbreak severity to assign stand vulnerability estimates (MacLean *et al.* 2001). The results of our work suggest that more accurate estimates of stand vulnerability could be obtained if the impacts of surrounding forest landscape composition were also taken into account.

3.8 Acknowledgements

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Liens: L'article précédent a souligné la nécessité de considérer le contexte spatial des peuplements du sapin baumier pour évaluer leur vulnérabilité aux épidémies de la tordeuse des bourgeons de l'épinette. En particulier, les résultats de cette étude ont montré que les diminutions de croissance radiale des hôtes dans les peuplements matures sont moins sévères quand le pourcentage des peuplements feuillus dans la mosaïque forestière est plus élevé. Dans l'article suivant nous avons examiné les patrons de mortalité des hôtes en relation avec la présence de feuillus dans le paysage. Ces deux études fournissent des informations fondamentales sur les patrons de diminutions de croissance, et sur les patrons de mortalité éventuelle des hôtes. Afin de bien comprendre les patrons de succession potentielle dans la forêt après les épidémies de la tordeuse des bourgeons d'épinette, les patrons spatial et temporel de mortalité des hôtes ont été examinés.

4 ARTICLE III - PATTERNS OF BUDWORM-CAUSED TREE DEATHS IN RELATION TO THE HARDWOOD CONTENT OF BOREAL FOREST LANDSCAPES

(Manuscrit en révision pour Ecoscience)

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4.1 Résumé

Afin d'évaluer l'influence de la répartition spatiale des peuplements sur la vulnérabilité des peuplements soumis à la dernière épidémie de tordeuse des bourgeons d'épinette (*Choristoneura fumiferana* Clem., Lepidoptera : Tortricidae) ayant eu lieu dans le nord-ouest Québécois (1971-1985), les patrons de mortalité des arbres en relation avec la présence de feuillus dans le paysage ont été étudiés dans un rayon de 1 km pour 31 peuplements dominés par le sapin baumier et l'épinette blanche. Alors que le sapin baumier (*Abies balsamea* (L.) Mill.) est 5 fois plus susceptible de mourir suite à une épidémie de tordeuse des bourgeons d'épinette que toutes autres espèces, le pourcentage de sapin tué varie considérablement parmi les peuplements (9-100%). Des analyses de régression indiquent qu'une proportion significative de cette variation (i.e. 18-25%) est expliquée par la présence de feuillus dans l'environnement immédiat des peuplements, le pourcentage de sapins morts diminuant significativement dans les peuplements à forte présence de feuillus à proximité. Cependant, le diamètre des arbres tend à masquer cet effet de la présence de feuillus dans le paysage. Alors que les gros sapins (> 20 cm) ont tous le même risque de mourir durant les épidémies, les plus petits sont dans 20% des cas moins susceptibles de mourir dans des peuplements entourés par des forêts feuillues. Les patrons temporels de mortalité des arbres varient également selon la présence de feuillus dans le paysage. Alors que la plupart des sapins ont été tués en 1984 dans les paysages contenant moins de 50 % de feuillus, les peuplements entourés de plus de feuillus ont connu aussi de la mortalité mais sur une plus longue période. La variabilité des patrons de mortalité du sapin baumier qui a été observée est susceptible d'entraîner des trouées dans la forêt pouvant varier considérablement quant à leurs tailles et taux de formation, ceci pouvant avoir d'importantes implications dans les patrons de succession de la forêt suivant des épidémies de tordeuse des bourgeons d'épinette.

Mots clés: sapin baumier, perturbation, mortalité, croissance, composition du paysage, tordeuse des bourgeons d'épinette

Nomenclature: Marie-Victorin, Fr., L. 2002.

4.2 Abstract

To evaluate the influence of stand spatial context on vulnerability of stands during the last spruce budworm (*Choristoneura fumiferana* Clem. [Lepidoptera: Tortricidae]) outbreak in northwestern Québec (1971-1985), we studied patterns of tree deaths in relation to the hardwood content of forest landscapes (%) within 1 km of 31 fir/spruce-dominated stands. While balsam fir, *Abies balsamea* [L.] Mill, was at least five times more likely to die following a budworm outbreak than any other tree species, the percentage of fir killed varied considerably (9-100%) among stands. Linear regression analyses indicated that a significant proportion of this variation (i.e., 18-25%) could be explained by the hardwood content of surrounding landscapes — the percentage of dead fir decreased in stands as landscape hardwood content increased. However, tree diameter confounded the effect of landscape context. While the frequency of balsam fir killed by budworm outbreaks was the same for large trees, regardless of landscape hardwood content, small trees were about 20% less vulnerable in stands surrounded by hardwood forests. Temporal patterns of tree deaths also varied with landscape hardwood content; while most balsam fir were killed about 1980 and 1984 in landscapes with <50% hardwood forests, fir surrounded by hardwood landscapes died over a longer period of time. The varying patterns of budworm-caused balsam fir deaths we found are likely to generate forest openings that vary considerably with respect to size and rate of formation, and this could have significant implications for forest succession following budworm outbreaks.

Keywords: balsam fir, forest disturbance, mortality, growth, landscape composition, spruce budworm

Nomenclature: Marie-Victorin, Fr., L. 2002.

4.3 Introduction

Periodic outbreaks of spruce budworm (*Choristoneura fumiferana* Clem.) (Lepidoptera: Tortricidae) are natural biotic disturbances in boreal and mixedwood forest regions of eastern North America. Spruce budworm larvae feed preferentially on the youngest available foliage of balsam fir (*Abies balsamea* [L.] Mill.) or spruce (*Picea* spp.) and during population outbreaks, repeated annual defoliation can kill a significant proportion of the host trees in a stand (Bergeron *et al.* 1995). Even though budworm outbreaks occur synchronously over large regions, local variations in timing, duration, and amplitude of population outbreaks occur (Royama *et al.* 2005). Combined with differences in the ability of hosts to withstand a given amount of defoliation, these variations in budworm outbreak dynamics can generate varying patterns of host tree deaths within and among stands.

Many researchers report that budworm-caused tree deaths are more frequent among hosts growing poorly-drained, or excessively dry sites, than on sites of intermediate soil moisture content (Hix *et al.* 1987; Osawa 1989; Dupont *et al.* 1991). However, studies relating host deaths during budworm outbreaks to stressful growing conditions have produced inconsistent results (Martinat 1987). The largest and oldest host trees in a stand are generally most vulnerable to spruce budworm outbreaks (MacLean 1980; Bergeron *et al.* 1995; Nealis and Régnière 2004). Stands dominated by balsam fir are more vulnerable to budworm than stands dominated by spruce (Harper *et al.* 2003; Bouchard *et al.* 2005) or stands where hosts are mixed with non-host softwoods like white cedar (*Thuja occidentalis* L.), jack pine (*Pinus banksiana* Lamb.) and various hardwoods (Bergeron *et al.* 1995).

Researchers have more recently acknowledged that the spatial context of a stand may significantly influence the severity of insect outbreaks (Kouki *et al.* 1997; MacKinnon and MacLean 2003). Two studies conducted in the boreal forest of northwestern Québec evaluated the influence of surrounding forest landscape composition on stand vulnerability to budworm outbreaks. Bergeron *et al.* (1995) found

that 14% fewer balsam fir were killed in fir-spruce stands in mixedwood landscapes than in landscapes dominated by softwood forests, and Cappuccino *et al.* (1998) found that 35% more balsam fir were killed in softwood-dominated landscapes than in fir-spruce habitat islands located in hardwood-dominated forest landscapes. Based on a small number of independent samples, however, these studies were intended to represent only a preliminary evaluation of landscape effects. The objective of this study was to build on these initial findings and determine how patterns of host deaths following the last budworm outbreak in this region (1974–1985) varied along a gradient of landscape hardwood content. We hypothesized that the percentage of dead hosts in fir-spruce stands would decrease as the percentage of hardwood stands in surrounding forest landscapes increased. We also examined temporal patterns in tree death related to the hardwood content of surrounding landscapes.

4.4 Methods

4.4.1 Study area

The study took place in and around the Lac Duparquet Research and Teaching Forest, which is located in the southeastern portion of the Canadian boreal forest near the Quebec-Ontario border (48°30'N, 79°25'W). The landscape in this region alternates between rolling hills with moraine deposits and lowlands covered by clays from the post-glacial lakes (Vincent and Hardy 1977). Data from a nearby weather station indicate a characteristically cold boreal climate, with a mean annual temperature of 0.6°C and mean annual precipitation of 823 mm. The mean annual frost-free period is 64 days but freezing temperatures can occur at any time throughout the year (Environment Canada 2000).

In the southern boreal zone, forested landscapes are complex mosaics of stands whose composition is related primarily to surficial deposits and successional stage (Bergeron and Dubuc 1989; Bergeron 2000). On mesic sites of clay deposits, early

successional stands (<100 years old) are dominated by trembling aspen (*Populus tremuloides* Michx), mid-seral stands (100-200 years) by balsam fir, paper birch (*Betula papyrifera* Marsh.), and white spruce (*Picea glauca* [Moench] Voss), and late-seral stands by balsam fir and white cedar with a lesser component of white spruce. On drier sites of moraine deposits, paper birch dominates early successional stands. Mid-seral and late-successional stands are dominated by the same species that occur on clay deposits but these drier sites usually have more black spruce (*Picea mariana* [Mill.] B.S.P) than white spruce. Early and mid-successional stands on bedrock are dominated by black spruce and jack pine or red pine, with white cedar becoming more abundant as stands age. Bogs and other hydric sites are dominated by black spruce, white cedar, and tamarack (*Larix laricina* [Du Roi] K. Koch.). Black ash (*Fraxinus nigra* Marsh.) and American elm (*Ulmus Americana* L.) dominate floodplains.

While selective logging of white spruce and white pine (*Pinus strobus* L.) has occurred throughout the study area since the early 1800s, more intense clear-cutting of these forests began in 1978 (Harvey and Bergeron 1989). Most of the early successional stands were initiated by stand-replacing wildfires in 1923 and 1944 (Dansereau and Bergeron 1993). The oldest stands in the study area were initiated from fires in 1717 and 1760. Periodic spruce budworm outbreaks have occurred in these forests since for at least 200 years — the last one in our study area occurred from 1974 to 1985 (Ressources naturelles Québec, *unpubl. data*).

4.4.2 Stand selection and sampling

Québec ecoforestry maps (1:20 000), based on 1983 aerial surveys, were used to identify potential sample stands in the study area. Ecoforestry maps delineate individual map polygons and assign them a unique set of attributes including: a stand identifier, species composition, species percentages, crown closure, height class, maturity class, and soil drainage class. To control for the influence that within stand hardwood content may have on stand vulnerability to budworm outbreaks (Bergeron *et al.* 1995), we first

identified all fir/spruce-dominated stands (i.e., stands with >75% fir/spruce and <25% hardwoods) located within about a 10 000 km² area centred on the Lac Duparquet Research and Teaching Forest. From this set of stands, we stratified sampling to ensure we captured a gradient in the hardwood content of forest landscapes within 1 km of each stand. We visually estimated landscape hardwood content using ecoforestry and fire history maps (Dansereau and Bergeron 1993). Selected fir-spruce stands were grouped into three broad landscape categories: 1 – *hardwood landscapes* disturbed by fire less than 100 years ago and covered largely (>75%) by hardwood stands in which paper birch or trembling aspen were the dominant species, 2 – *softwood landscapes* have remained undisturbed by fire for more than 200 years and covered largely by spruce/fir-dominated stands and <25% hardwood-dominated stands, 3 – *mixed landscapes* had less extensive recent fires than deciduous landscapes and thus anywhere from 25 to 75% of the landscape was covered by deciduous-dominated stands. Prioritizing potential sample stands by proximity to roads, or the shore of Lac Duparquet, we sampled at least five stands in hardwood and softwood landscapes, and at least 10 stands in mixedwood landscapes, because the range of hardwood content was greater (i.e., 25–50%). A total of 31 stands were sampled between 1998 and 2000. Portions of the ecoforestry maps were digitized and ArcView GIS was used to calculate more accurate values for the hardwood content of landscapes (%) within 1 km of sampled stands, which ranged from 1 to 83% (median = 50%).

Local stand characteristics were quantified in a 20 x 20 m plot located at the centroid of each stand. The diameter of all trees (living and dead) taller than >1.3 m was tallied into 5 cm diameter classes. Both standing and downed dead trees were counted. However, downed trees were counted only if decomposition was minimal (i.e., trees had branches and bark remaining permitting species identification).

Increment cores were obtained from canopy dominant balsam fir and white spruce (>15 cm d.b.h) in each stand; the first 10 trees closest to the plot centre were selected for sampling. Basal disks were also cut from up to 10 dead balsam fir that were closest to the plot centre. Increment cores and discs were prepared in the laboratory following

standard dendrochronological techniques (Stokes and Smiley 1968). Tree rings were measured to the nearest 0.001 mm and assigned dates that were verified using cross-dating procedures (Holmes 1983). Tree-ring data were used to date balsam fir deaths, estimate tree ages, and determine how tree growth varied among stands. All discs cut from dead trees had bark on at least a portion of the sample, permitting identification of the outermost tree-ring needed for dating tree deaths.

4.4.3 Data analyses

Least squares linear regression analyses were used to test for relationships between the percentage of dead balsam fir in stands and the percentage of hardwood forests, within a 1 km landscape, surrounding each stand. A total of nine regression models were evaluated. Separate analyses were conducted on three dependent variables: i) percentage of balsam fir >5 cm d.b.h that were dead; ii) percentage of balsam fir >10 cm d.b.h dead; and, iii) percentage of balsam fir >15 cm d.b.h. dead. By considering only tree deaths among trees greater than 5 cm d.b.h, we reduced the chance of including trees killed due to intense competition for light in the subcanopy. Because most budworm-killed trees fall and decay before the occurrence of another outbreak (Lambert *et al.* 1980) and annual mortality between budworm outbreaks is relatively low (MacLean and Ostaff 1989), we think we have not significantly over-estimated tree deaths associated with the last budworm outbreak by counting standing dead and downed balsam fir with remaining bark and branches. For each of three dependant variables, we tested the influence of three landscape variables separately: the percentage of landscape area covered by all hardwood dominated forests (TDEC_LAND), the percentage of landscape area covered by paper birch-dominated forests (BB_LAND), and the percentage of landscape area covered by trembling aspen-dominated forests (PE_LAND). Normality and homogeneity of variance assumptions of regression models were examined using plots of residuals and formally tested using Durbin-Watson and White's moment specification test statistics, respectively.

4.5 Results

4.5.1 Overall patterns of tree deaths

Fifty-three per cent of balsam fir were dead over all of the 31 stands sampled. Dead balsam fir were proportionately much more abundant than dead trees of any other species (Figure 4.1). Only about 9% of white spruce and no black spruce (the two other budworm hosts) were dead. The proportion of dead white spruce was similar to that of dead paper birch (7%), a species that is not a host to spruce budworm. Deaths of white cedar and trembling aspen were < 1%.

In our study area, the percentage of dead balsam fir in stands was not only much higher but it varied considerably more (9–100%) among stands than deaths of white spruce (0–33%). Because deaths of spruce, and other non-host trees, following budworm outbreaks were relatively rare, further analyses, which examined influences of hardwood content in surrounding landscapes on tree deaths, focused on balsam fir.

4.5.2 Stand characteristics and balsam fir deaths

Although ecoforestry maps indicated the stands we sampled had >75% fir-spruce, and <25% hardwoods, field surveys indicated somewhat more variation in stand composition (Table 4.1). Together, balsam fir and spruce comprised <75% of the total tree density in 11 of the 31 sampled stands. While 5 of these stands had more white cedar than expected (i.e., 32% to 61% of total tree density), another 5 stands had more hardwood species than expected (i.e., 26% to 38%). One stand had 57% host species and about 20% each of white cedar and hardwoods. Even though budworm hosts did not comprise >75% of total tree density in 11 stands, they were still the dominant species (>50%) in all but 2 stands, and balsam fir was always more abundant than spruce.

We thought that the larger than expected variation in stand hardwood content (or other tree species), and variations in balsam fir vigour (Table 4.1), might generate a gradient in the percentage of dead balsam fir in stands that could obscure an effect of

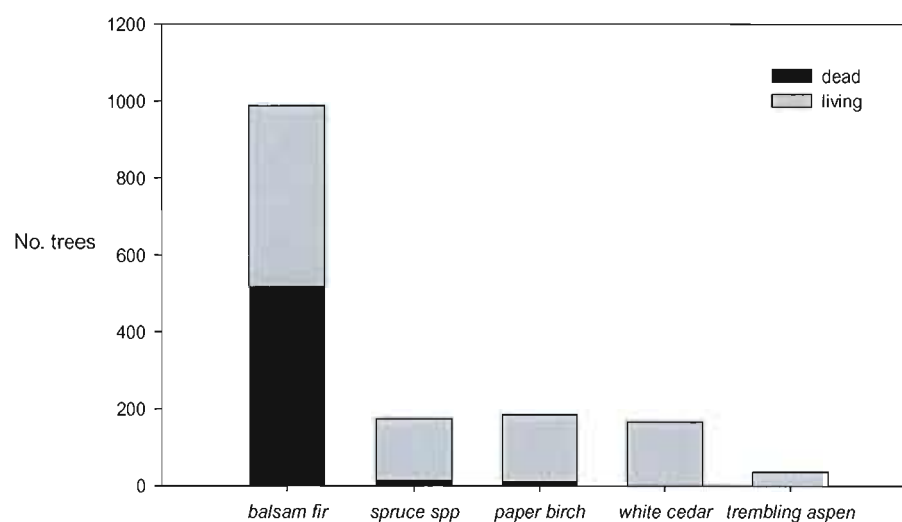


Figure 4.1. Total number of living and dead balsam fir (*Abies balsamea*), spruce (*Picea glauca* and *P. mariana*), paper birch (*Betula papyrifera*), white cedar (*Thuja occidentalis*), and trembling aspen (*Populus tremuloides*) over all 31 stands sampled in northwestern Québec.

Table 4.1. Characteristics of 31 stands sampled in the boreal zone of northwestern Quebec.

Stand No.	Mean annual increment of balsam fir *	Total tree density [†] (stems/ha)	Stand composition (% total tree density)				Surrounding landscape composition (% hardwood forests)
			BF [‡]	HOST	TO	HW	
1	3.58	1797	48	93	0	7	1
2	2.20	3672	45	65	8	27	3
3	1.91	4253	75	78	9	13	7
4	3.34	938	71	88	0	13	9
5	1.87	2500	31	34	61	5	16
6	1.62	1327	71	94	0	6	17
7	2.51	977	60	76	0	24	17
8	2.00	2029	77	85	0	15	24
9	2.27	1523	41	41	54	5	24
10	1.71	1211	45	84	0	16	30
11	2.43	2262	98	98	0	2	33
12	2.37	1523	90	90	3	8	34
13	2.34	2852	81	100	0	7	41
14	1.92	1561	92	64	0	0	46
15	1.88	1094	61	62	32	4	49
16	1.79	3125	62	57	35	3	50
17	1.92	1913	53	70	20	22	53
18	2.40	2773	68	76	14	15	53
19	1.95	1796	65	62	24	0	55
20	1.74	1016	35	83	0	38	56
21	2.62	3463	82	90	14	4	56
22	1.74	1873	90	93	0	10	64
23	1.79	1563	85	62	5	3	65
24	2.42	2070	57	98	0	38	66
25	2.33	1912	88	100	0	2	67
26	1.95	1601	78	67	0	0	68
27	2.13	2226	39	95	0	33	71
28	1.85	1561	85	90	0	5	75
29	1.84	1600	78	100	0	10	76
30	2.47	1717	98	69	0	0	80
31	2.06	1366	66	93	6	26	83

* average annual radial growth increment (mm) of balsam fir over a 10 year period between the last outbreak and the one previous to that (i.e., 1955-1965)

[†] density of live and dead trees greater than 5 cm diameter at breast height (1.3 meters).

[‡] BF= Balsam fir; HOST= all budworm hosts, including balsam fir and spruce spp. (*Picea glauca* and *P. mariana*); TO = non-host softwoods (i.e., *Thuja occidentalis*); HW = all hardwoods (*Betula papyrifera* and *Populus tremuloides*)

surrounding landscape hardwood content. To account for this possibility, the percent hardwood content of stands (TDEC_STAND; which was predominantly paper birch) and balsam fir vigour (BF_VIGOUR) were included as covariables in multiple regression analyses. However, for all of the nine multiple regression models examined, these stand variables did not explain a significant portion of the variation in the percentage of dead balsam fir among stands (Table 4.2).

4.5.3 *Landscape hardwood content and balsam fir deaths*

In contrast to stand variables, surrounding landscape composition did have a significant influence on the percentage of balsam fir killed by the last spruce budworm outbreak (Table 4.2). However, the only landscape variable with a significant effect ($p < 0.10$) was TDEC_LANDSCAPE (i.e., multiple regression models 1, 4, and 7) (Table 4.2) — the percentage of paper birch- (BB_LANDSCAPE) or trembling aspen-dominated (PE-LANDSCAPE) stands that covered boreal landscapes made no significant contribution to variation in the percentage of dead balsam fir observed in stands (Table 4.2). Thus, stands following budworm outbreaks. Despite a statistically significant effect of TDEC_LANDSCAPE, relationships between the percentage of dead balsam fir in stands and TDEC_LANDSCAPE became progressively weaker as fewer small trees were included in % dead fir measurements in stands (Table 4.2), indicating a confounding effect of tree diameter. While TDEC_LANDSCAPE accounted for about 25% of the variation in deaths of balsam fir deaths among trees greater than 5 cm d.b.h. (Figure 4.2), it accounted for about 23% and 18% of balsam fir deaths among trees greater than 10 cm d.b.h. and greater than 15 cm d.b.h., respectively (Table 4.2).

We further examined the confounding effect of tree diameter on the relationship between percentage of dead balsam fir stands and hardwood content of surrounding landscapes by dividing stands into two landscape types, those surrounded by landscapes covered by >50% hardwood-dominated stands (>50%TDEC_LANDSCAPE) and those surrounded by landscapes covered by <50% hardwood-dominated stands

Table 4.2. Summary of multiple linear regression analysis ($n = 31$). The dependant variable, percentage of dead balsam fir in stands, was stratified by diameter class to consider: deaths of balsam fir >5 cm d.b.h, > 10 cm d.b.h and >15 cm d.b.h. Independent variables describe: (a) landscape hardwood content (%) within 1 km of stands (TDEC_LANDSCAPE = percentage of landscape covered by hardwood-dominated stands of all species; BB_LANDSCAPE = % landscape covered by paper birch-dominated stands, PE_LANDSCAPE = % landscape covered trembling aspen-dominated stands), (b) the percent hardwood content (all species) of stands (TDEC_STAND), and (c) mean balsam fir vigour in the stands sampled (BF_VIGOUR).

Model No.	Dependent variable ^a	Intercept	R ²	MSE	Independent variables	Regression coefficient	p
1	% dead fir >5 cm d.b.h ^b	99.31	0.25	22.95	TDEC_LANDSCAPE	-0.50	0.007
					TDEC_STAND	-3.01	0.247
					BF_VIGOUR	-69.48	0.760
2	% dead fir >5 cm d.b.h	84.10	0.06	25.67	BB_LANDSCAPE	-23.92	0.265
					TDEC_STAND	-2.63	0.916
					BF_VIGOUR	-0.94	0.354
3	% dead fir >5 cm d.b.h	94.07	0.10	25.24	PE_LANDSCAPE	-46.40	0.144
					TDEC_STAND	-2.6	0.914
					BF_VIGOUR	-91.01	0.213
4	% dead fir >10 cm d.b.h	100.07	0.23	27.69	TDEC_LANDSCAPE	-0.36	0.087
					TDEC_STAND	-10.65	0.691
					BF_VIGOUR	-86.72	0.249

Table 4.2 (cont.)							
5	% dead fir >10 cm d.b.h	90.06	0.05	28.89	BB_LANDSCAPE	-19.69	0.412
					TDEC_STAND	-10.87	0.701
					BF_VIGOUR	-84.25	0.286
6	% dead fir >10 cm d.b.h	95.68	0.07	28.78	PE_LANDSCAPE	-33.25	0.353
					TDEC_STAND	-10.42	0.715
					BF_VIGOUR	-101.78	0.222
7	% dead fir >15 cm d.b.h	1.80	0.18	0.43	TDEC_LANDSCAPE	-0.01	0.074
					TDEC_STAND	-0.28	0.511
					BF_VIGOUR	-1.94	0.107
8	% dead fir >15 cm d.b.h	1.67	0.12	0.46	BB_LANDSCAPE	-0.40	0.291
					TDEC_STAND	-0.30	0.502
					BF_VIGOUR	-1.94	0.124
9	% dead fir >15 cm d.b.h	1.74	0.11	0.46	PE_LANDSCAPE	-0.58	0.306
					TDEC_STAND	-0.27	0.535
					BF_VIGOUR	-2.21	0.098

^a Regression analyses were performed on an arcsine square-root transformation of the dependant variable %dead fir >15 cm d.b.h.

^b Regression analyses were performed on an arcsine square-root transformation of BB_LANDSCAPE and TDEC_STAND and a log transformation of BF_VIGOUR.

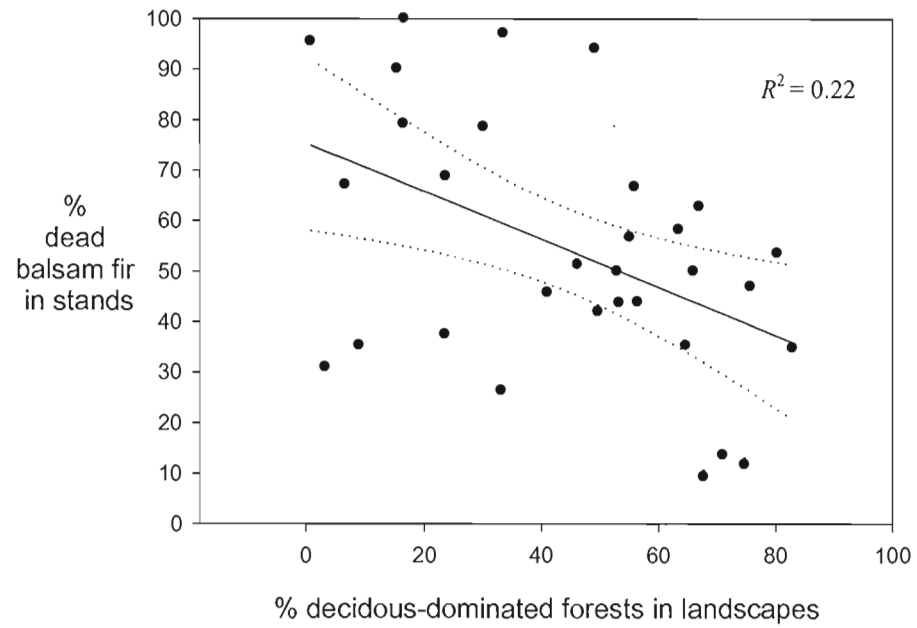


Figure 4.2. Linear regression relationship between the percentage of balsam fir (> 5 cm d.b.h.) killed in stands and the hardwood content of surrounding forest landscapes in Quebec.

(<50%TDEC_LANDSCAPE), and tree size by 5 cm diameter classes (Figure 4.3). The percentage of balsam fir killed did not significantly differ among landscape types when trees were larger than 20 cm d.b.h. (Figure 4.3) However, among trees smaller than 15 cm, the percentage of dead balsam fir was significantly lower, by about 10 to 20 per cent, in landscapes composed predominantly of hardwood stands (Figure 4.3).

Balsam fir deaths were recorded for 23 years after the onset of the last spruce budworm outbreak in 1971. Frequency distributions showing the percentage of dead balsam fir, by 5-year periods, illustrate important differences in temporal patterns related to landscape type (Figure 4.4). Among landscapes comprised of less than 50% hardwood forests (<50% TDEC_LANDSCAPE), most trees died between 1980 and 1984, the period of time during which maximum budworm-caused growth reductions were also observed (i.e., 1982-1984; see Chapter 3). While many balsam fir deaths also occurred from 1985 and 1989, overall most balsam fir (57%) died before the outbreak crashed in 1985 (Annex 9.1). The patterns of balsam fir deaths among landscapes dominated by deciduous forests (>50% TDEC_LANDSCAPE) was considerably different with about the same percentage of trees dying each 5-year period from 1980 to 2000 and most trees (70%) dying after the outbreak crashed in 1985.

4.6 Discussion

By restricting sampling to fir/spruce-dominated stands, this study was controlled for the influence that stand composition – in particular, the hardwood content of stands – had on the percentage of balsam fir killed by spruce budworm outbreaks. While Quebec ecoforestry maps were used to select stands containing > 75% fir/spruce and < 25% hardwoods, later analysis of field survey data indicated greater variation in stand composition than expected, with 0 to 38% hardwoods. This discrepancy is probably due, in part, to aerial photo-interpretation errors made during the mapping process. The fact

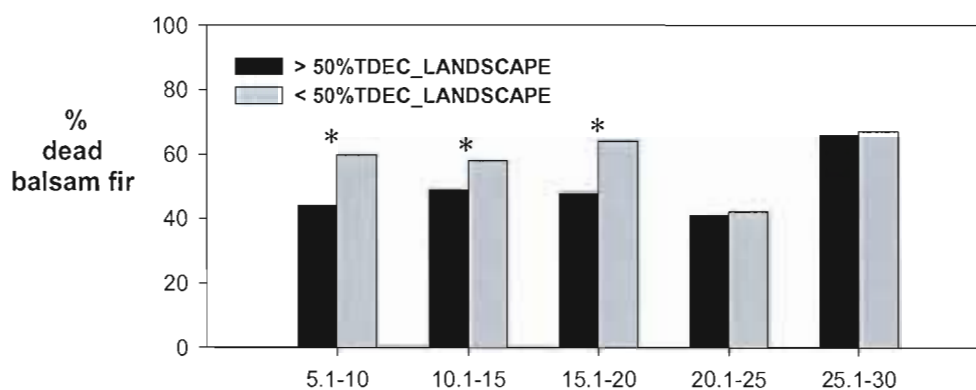


Figure 4.3. Percentage of budworm-killed balsam fir, by diameter class, in relation to the hardwood content of surrounding landscapes. Landscape hardwood content is divided into two classes: >50% TDEC_LANDSCAPE = > 50% of landscape covered by hardwood-dominated forests, and <50% TDEC_LANDSCAPE = < 50% of the landscape is covered by hardwood-dominated forests. Within each diameter class, a 2x2 contingency table analysis was conducted to determine if there were significantly more dead fir in each landscape class. Asterisks above filled bars indicate significant differences ($p < 0.05$).

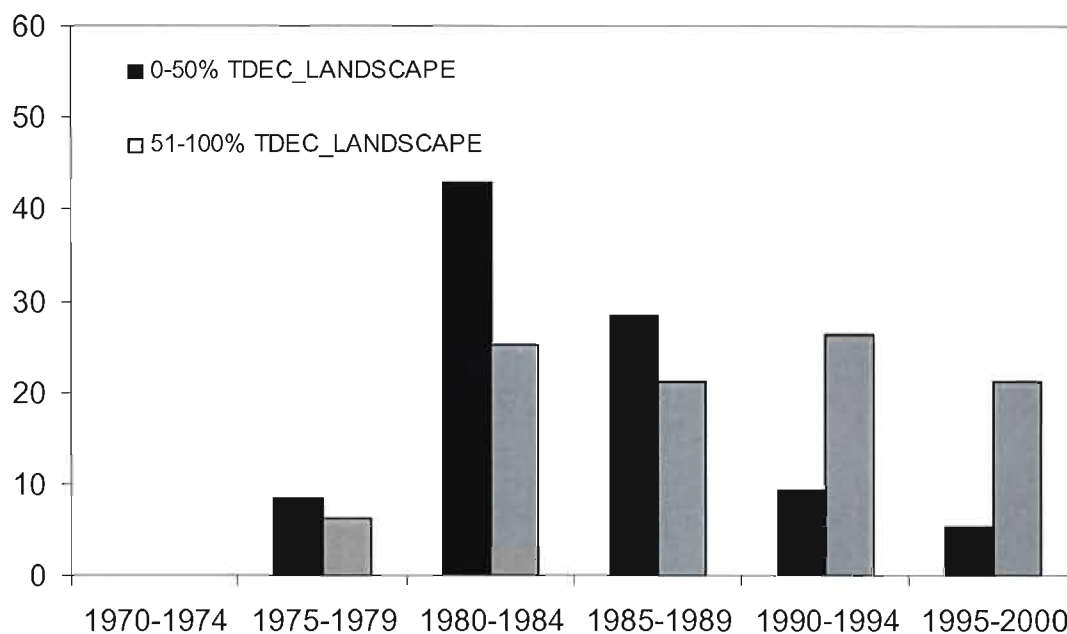


Figure 4.4. Temporal patterns of balsam fir (*Abies balsamea*) deaths in relation to the hardwood content of surrounding forest landscapes. The percentage of balsam fir killed were recorded for six, five-year periods. Landscape hardwood content is divided into two classes: >50% TDEC_LANDSCAPE = > 50% of landscape covered by hardwood-dominated forests, and <50% TDEC_LANDSCAPE = < 50% of the landscape is covered by hardwood-dominated forests.

that we found no significant relationship between this gradient in stand hardwood content and the percentage of dead balsam fir in stands indicates that a stand hardwood content up to 38% is still not sufficiently high enough to reduce stand vulnerability to budworm outbreaks and suggests that some threshold level of stand hardwood content is required to elicit an effect. This finding is consistent with Su *et al.* (1996), who found significantly lower budworm defoliation levels in stands only when the hardwood content of stands was greater than 40%.

The hardwood content of surrounding forest landscapes, which varied much more than stand hardwood content, was significantly related to spruce budworm outbreak severity in stands. As the hardwood content (%) of forest landscapes increased, the percentage of trees in a stand killed by budworm decreased. This result is consistent with previous stand- and landscape-level research indicating that forests with more hardwoods are less defoliated, and contain fewer budworm-killed trees, than host-dominated forests (MacLean 1980; Bergeron *et al.* 1995; Su *et al.* 1996; Cappuccino *et al.* 1998; Bouchard *et al.* 2005). It also supports a long history of studies indicating that forest composition influences the severity of insect outbreaks (*cf.* Miller and Rusnock 1993; Jactel *et al.* 2005; Koricheva *et al.* 2006). Two major hypotheses can be proposed to explain the lower percentage of balsam fir deaths in stands surrounded by hardwood-dominated forest landscapes. First, it is possible that the initial densities of budworm in these stands were lower simply because dispersing moths were less likely to find these isolated habitat islands. However, pheromone trap experiments in our study area have shown that male moths were just as abundant in contiguous tracts of balsam fir forests as they were in balsam fir stands isolated by hardwood forests (Cappuccino *et al.* 1998). Although adult male densities do not necessarily reflect female abundance or oviposition rates, these results do suggest that differences in initial budworm densities are an improbable explanation for our findings. A second, and more plausible, explanation for the lower tree deaths in spruce-fir stands in hardwood-dominated landscapes is that these stands contain more abundant, and a more diverse complex of, budworm natural enemies. Parasitism of budworm eggs, larvae and pupae, by various species of

Tachinids, ichneumonids, and hymenoptera, is greater in mixedwood forests (Cappuccino *et al.* 1998; Quayle *et al.* 2003). More abundant nectar sources and alternate hosts associated with greater forest hardwood content likely explain the higher parasitoid densities and rates of parasitism that help to suppress budworm populations (Simmons *et al.* 1975; Houseweart *et al.* 1984). Larval predation by a potentially more diverse community of birds, particularly in mixedwood landscapes, may also be a contributing factor (Crawford and Jennings 1989; Drapeau *et al.* 2000).

We suspect that differences in tree mortality between size classes is because budworm adult moths generally colonize and oviposit on large, canopy dominant hosts first (Blais 1953; Greenbank *et al.* 1980), with early larval stages beginning to feed on the foliage of these trees and later larval stages dispersing downward in the forest canopy when competition for food becomes intense. The fact that fewer small balsam fir were killed in stands surrounded by hardwood landscapes may be because higher budworm parasitism rates in these stands are keeping budworm populations low enough to reduce competition and thus the pressure for larvae to disperse.

While Blais (1981) found that most host mortality occurred within a few years after budworm outbreaks ended, others report that balsam fir trees can remain weakened and die over much longer periods of time (Filion *et al.* 1998; Kneeshaw and Bergeron 1999; Bouchard *et al.* 2005). In our study, both of these temporal patterns in tree deaths occurred. Whereas most balsam fir died within a single 5-year period when stands were part of extensive tracts of fir-spruce forests, balsam fir in stands surrounded by hardwood-dominated landscapes died over a much longer period. We suspect that this can at least partly be explained by temporal differences in cumulative defoliation levels among these stands. While spruce budworm feeds almost entirely on current year's foliage, it is the cumulative amount of defoliation occurring over a period of years that determines tree survivorship (Erdle and MacLean 1999). The fact that trees in fir-spruce stands of host-dominated landscapes died over a shorter period of time than in stands of hardwood-dominated landscapes suggests that annual defoliation was more severe and thus the threshold level of cumulative defoliation required to kill a tree was attained

sooner. This supposition is supported by studies of balsam fir growth decline during spruce outbreaks in northwestern Quebec — radial growth reductions resulting from defoliation during the last outbreak in this region were much more severe, and of longer duration, as the hardwood content of surrounding landscapes decreased (Campbell *unpublished data*). Once again, higher levels of parasitism in stands surrounded by hardwood landscapes may contribute to lower defoliation. To our knowledge, no other studies have examined relationships between forest composition and temporal patterns of budworm-caused host deaths. However, MacLean (1980) did observe analogous temporal patterns in tree deaths among different aged stands where tree deaths in mature balsam fir stands occurred within 4-5 years of the start of an outbreak whereas deaths of trees in immature stands occurred after 7-8 years and lasted up to 12 years.

Disturbances caused by spruce budworm outbreaks are an important driving force of change in boreal forests of eastern Canada (Bergeron 2000). Budworm outbreaks generate forest openings that vary their size and rate of formation (Kneeshaw and Bergeron 1998; D'Aoust *et al.* 2004). Based on the results of our study, we propose that patterns of balsam fir deaths related to forest hardwood content could generate variations in the physical characteristics and rate of opening formation having important implications for successional trajectories following budworm outbreaks. For example, among mature balsam fir stands in spruce/fir-dominated landscapes, rapid deaths of mature canopy fir and subcanopy trees may generate vertically deep and fast-forming gaps that provide establishment opportunities for shade-intolerant species. If shade-intolerant tree species are present in the pre-disturbance stand, mature balsam fir stands may be converted to mixedwood stands characteristic of earlier seral stages and if shade-intolerant species are absent, colonization of shrubby species, like mountain maple (*Acer spicatum* Lam.) may lead to a retrogressive successional process. Among mature balsam fir stands in hardwood-dominated landscapes, slower deaths of mature canopy fir and low rates of subcanopy tree death may result in vertically shallow and slow-forming gaps that provide little opportunity for shade-intolerant species to colonize. In these cases, if advance balsam fir regeneration is abundant in the understory succession may

be cyclical; otherwise, budworm outbreaks may accelerate the successional process with highly shade-tolerant white cedar becoming more prominent. Similar successional trajectories following budworm outbreaks have been described in other studies (Baskerville 1975, MacLean 1988; Morin 1994; Kneeshaw and Bergeron 1998; Bergeron et al. 2000; Bouchard et al. 2005).

4.7 Conclusions

Spruce budworm outbreaks have occurred in fir-spruce forests for millennia (Simard *et al.* 2002; 2006) and through their ability to cause tree deaths during outbreaks, they play an important role in restructuring forests to drive forest succession, promote nutrient cycling, and maintain biological diversity. While their ecological role remains unchanged through history, some researchers postulate that budworm outbreaks have become more frequent and extensive over the last two centuries in eastern Canada (Blais 1983; Jardon *et al.* 2003; Simard *et al.* 2006). The last spruce budworm outbreak significantly reduced wood supplies, generating substantial socioeconomic losses (Power 1991; National Forest Database 1995). Many researchers have suggested that silvicultural activities altering forest composition could be used to reduce the impacts of spruce budworm outbreaks on timber supplies (Miller and Rusnock 1993). The findings of our study support this long-held view. While forest managers currently rely on local stand characteristics to predict stand vulnerability to future budworm outbreaks (MacLean *et al.* 2001), our results indicate that incorporating information about the spatial context of stands (i.e., influence of surrounding landscape hardwood content) on patterns of host death following outbreaks will provide forest managers with an improved basis for assessing stand vulnerability and managing forests to minimize the economic impact of budworm outbreaks. We propose that effects of surrounding hardwood content be incorporated into decision support tools, such as the Spruce Budworm Decision Support System (MacLean *et al.* 2001; 2002), so that more accurate predictions of stand vulnerability can be calculated and marginal timber supply benefits

of altering forest landscape hardwood content can be evaluated. In conclusion, our findings indicate that increasing the hardwood content of managed forest landscapes could help to reduce budworm outbreak impacts. Forest management plans designed to minimize the impact of budworm outbreaks should combine several strategies, like planting of non-host softwood species, harvest scheduling and silviculture (e.g., stand thinning), and judicious use of insecticides, with ways to increase forest hardwood content.

4.8 Acknowledgements

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Liens: Dans l'article II nous avons vu que les diminutions de croissance radiale des hôtes dans peuplements matures au Québec sont moins sévères quand le pourcentage des peuplements feuillus dans la mosaïque forestière est plus élevé. La prochaine étude a permis la possibilité d'examiner l'influence des épidémies de TBE sur la croissance radiale des hôtes dans un contexte différent soit au Nouveau-Brunswick. Contrairement au nord ouest Québécois, des programmes d'épandages d'insecticides ont été mis en opération au Nouveau-Brunswick afin de minimiser les impacts des épidémies sur les réserves de bois. Dans, le prochain article, nous avons comparé l'influence de la composition de la mosaïque forestière (i.e., le pourcentage des feuillus dans le paysage environnant les peuplements matures) et l'influence de l'épandage d'insecticides sur la sévérité des épidémies au Nouveau Brunswick.

5. ARTICLE IV - THE SEVERITY OF BUDWORM-CAUSED GROWTH
REDUCTIONS IN BALSAM FIR/SPRUCE STANDS VARIES WITH THE
HARDWOOD CONTENT OF SURROUNDING FOREST LANDSCAPES

(Manuscrit accepté à Forest Science)

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5.1 Résumé

Les données dendrochronologiques recueillies sur des sapins baumiers (*Abies balsamea* [L.] Mill.) dans 31 peuplements dominés par les épinettes (*Picea* spp.) et les sapins dans le nord du Nouveau-Brunswick ont permis de déterminer si la variation dans la réduction de la croissance radiale lors de la dernière épidémie de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.) (1972-1992) pouvait dépendre des facteurs suivants: l'abondance des peuplements dominés par des feuillus dans la mosaïque forestière, l'historique des pulvérisations d'insecticides et l'élévation. On a eu recours à l'analyse de régression pas à pas pour élaborer les 12 modèles décrivant les relations entre la réduction de la croissance moyenne (i.e., l'écart entre la croissance moyenne de l'arbre échelonnée à parts égales par rapport à la durée de vie de tous les arbres d'un peuplement) et des variables explicatives, pour les années où plus de 80% des peuplements ont enregistré une diminution de croissance (1976-1978, 1982-1984, 1990, 1991, 1994) de même que pour trois périodes de réduction de la croissance des arbres: 1972-1980, 1981-1985, et 1986-1993. L'abondance des peuplements feuillus dans la mosaïque forestière a été retenue dans tous les modèles de régression ($P < 0.05$) et a expliqué 12% à 41% de la variation dans la réduction de la croissance entraînée par la tordeuse. Les différences dans la diminution de la croissance entre les peuplements étaient plus marquées au cours des années initiales de l'épidémie de la tordeuse des bourgeons de l'épinette (1972-1980), particulièrement en 1976 lorsque les réductions moyennes furent de ~ 40% dans les peuplements des mosaïques forestières composées de <50% de feuillus et de ~ 20% dans les peuplements des mosaïques forestières composées de >50% feuillus. Les relations entre la variation dans la réduction de croissance entre les peuplements et l'élévation ou l'historique des pulvérisations d'insecticides étaient moins constantes que celles avec l'abondance de feuillus dans la mosaïque forestière. Nos résultats donnent à penser qu'augmenter l'abondance d'arbres feuillus dans la mosaïque forestière pourrait contribuer à réduire l'impact des épidémies sur les espèces résineuses commerciales.

Mots-clés: impact de la tordeuse des bourgeons de l'épinette, défoliation, dendroécologie, épidémies d'insectes

5.2 Abstract

Tree-ring data collected from balsam fir (*Abies balsamea* [L.] Mill.) in 31 spruce (*Picea* spp.) /fir-dominated stands in northern New Brunswick were used to evaluate how radial growth reductions during the last spruce budworm (*Choristoneura fumiferana* Clem.) outbreak (1972-1992) varied according to the hardwood content of surrounding forest landscapes, insecticide spray history and elevation. Stepwise regression analysis was used to build 12 models describing relationships between mean percent growth reduction (i.e., deviation from mean tree growth averaged over the lifespan of all trees in a stand) and the explanatory variables for years when greater than 80% of stands had growth reductions (1976-1978, 1982-1984, 1990, 1991, 1994) and for three growth reduction periods (1972-1980, 1981-1985, and 1986-1993). The hardwood content of surrounding forest landscapes entered into all significant regression models ($P < 0.05$), explaining 12 to 41% of the variance in budworm-caused growth reductions. Differences in growth reductions among stands were greatest during the initial years of the budworm outbreak (1972-1980), particularly in 1976 when mean reductions were ~ 40% in stands with <50% hardwood content and ~ 20% in stands where surrounding hardwood content was >50%. Relationships between variation in growth reductions among stands and elevation or insecticide spray history were weak and less consistent than with landscape hardwood content. Our findings suggest that increasing the hardwood content of forest landscapes could help to reduce the impact of outbreaks on timber supplies.

Keywords: budworm impacts, defoliation, dendroecology, insect outbreaks

5.3 Introduction

Periodic spruce budworm (*Choristoneura fumiferana* Clem.) (Lepidoptera: Tortricidae) outbreaks occur about every 35 years in the boreal and mixedwood forest regions of North America (Royama 1984; Jardon *et al.* 2003). During outbreaks, repeated annual defoliation by budworm larvae reduces tree growth and often kills its hosts, particularly balsam fir (*Abies balsamea* [L.] Mill.), over vast areas (MacLean 1980; Hardy *et al.* 1986; Bergeron *et al.* 1995). While budworm outbreaks are natural forest disturbances that play a critical role in directing large-scale ecological processes (e.g., forest succession and nutrient cycling), they also reduce timber supplies and generate substantial socio-economic losses. From 1977 to 1987, 17-22% of the annual timber harvest level was lost to spruce budworm in Canada (Sterner and Davidson 1982; Power 1991; National Forestry Database 1995).

During the spruce budworm outbreak of the 1970s, 1980s, and early 1990s, aerial application of insecticide was used throughout much of eastern Canada to reduce budworm damage and economic losses. Broad-spectrum chemical insecticides (e.g., fenitrothion), as well as the biological insecticide *Bacillus thuringiensis* (*B.t.*), were applied. While chemical insecticides are no longer considered an environmentally acceptable option for controlling insect outbreaks in Canada, *B.t.*, and the insect growth regulator, Mimic®, can be used to reduce budworm populations during outbreaks to protect foliage and prevent host deaths. Past management efforts to reduce the impact of spruce budworm outbreaks in eastern Canada have relied heavily on the application of insecticides but given concern about the potential negative ecological impacts of spraying – for example, dramatic reductions of Lepidoptera could significantly alter forest insect communities and affect a range of other species and ecosystem processes (Crawford and Jennings 1989; Miller 1990) – additional approaches to reducing economic impacts of budworm outbreaks are necessary.

The fact that damage caused by spruce budworm outbreaks varies with forest species composition has long been recognized. Based on these observations, researchers have proposed that silvicultural activities altering forest species composition could help

to reduce the impact of budworm outbreaks (Westveld 1946; Baskerville 1976; Blais 1983; Blum and MacLean 1984). While Miller and Rusnock (1993) suggested that there was little evidence to support this “silvicultural hypothesis”, citing fallacious assumptions and logistical problems associated with developing large-scale experimental tests, MacLean (1996) argued strongly against their conclusions, indicating that while budworm outbreaks cannot be prevented (Royama 1984; Royama *et al.* 2005), damage caused during outbreaks can be reduced through silviculture, and outcomes of various large-scale forest management scenarios can be tested, particularly with decision support systems that use empirical data to model budworm population dynamics, forest dynamics and stand vulnerability. MacLean (1996) proposed that alterations to forest composition to reduce budworm impacts could be attained through: i) planting non-host softwood species (e.g., jack pine, *Pinus banksiana* Lamb.); ii) selective harvesting of balsam fir in stands to increase the content of non-hosts or less vulnerable species (e.g., spruce); and, iii) clearcutting to break up balsam fir forests that are contiguous across landscapes.

Many recent studies that describe and quantify relationships between forest composition and budworm impact support the position of MacLean (1996). They indicate that stands dominated by balsam fir are more vulnerable to budworm outbreaks than those dominated by spruce (Harper *et al.* 2003; Bouchard *et al.* 2005) or stands where hosts are mixed with non-host softwoods like white cedar (*Thuja occidentalis* L.) and jack pine. The presence of various hardwoods in stands is also related to lower budworm impacts (Bergeron *et al.* 1995; Su *et al.* 1996), possibly because the natural enemies of spruce budworm are more abundant in mixed forests than in pure softwood stands (Cappuccino *et al.* 1998). In addition to local-scale effects of stand composition, a number of studies propose that surrounding forest landscape composition can also influence budworm outbreak impacts in stands (Bergeron *et al.* 1995; Cappuccino *et al.* 1998; Kouki *et al.* 1997). None of these studies, however, describe or quantify relationships between outbreak impacts and the hardwood content of surrounding landscapes. The objective of our work was to build on stand-level findings regarding the

influence of hardwoods (Bergeron *et al.* 1995; Su *et al.* 1996) and test the hypothesis that the impact of budworm outbreaks varies among stands according to the hardwood content of surrounding landscapes. In our analysis we also compare the effects of hardwood content with insecticide spraying. Whereas all of the aforementioned studies measured the impact of budworm outbreaks in terms of host defoliation or mortality levels in stands, we measured impacts in terms of average growth losses incurred among individual balsam fir trees in a stand. Growth losses of individual trees are directly related to the proportion of foliage removed by budworms (Erdle and MacLean 1999), and can reflect budworm population densities on individual trees. Traditionally, budworm impacts have been expressed as a spatially integrated landscape-scale measure of the extent of damage (i.e., hectares of defoliation calculated from aerial surveys) (e.g., Hardy *et al.* 1986). Studies such as this one, and others that quantify stand-level impacts based on measurements of individual trees (e.g., MacKinnon and MacLean 2004), better reflect local budworm population densities and thus provide an improved basis for understanding relationships between forest composition, outbreak impacts and the mechanisms that drive budworm population dynamics. This information could have significant implications for the way in which forests are managed to reduce future socioeconomic losses caused by budworm outbreaks.

5.4 Methods

5.4.1 Study area

Thirty-one stands were sampled in northern New Brunswick. Most stands occurred within the Northern Uplands bioclimatic ecoregion but a few stands occurred in the Highlands and the Central Uplands ecoregions (Figure 5.1). Elevations ranged from 177-549 m, with a mean of 335 m. The Northern Uplands is climatically intermediate to the colder Highlands and the warmer, wetter Central Uplands (TECWG 2003). Mean annual, seasonal, and monthly climate conditions were calculated for each stand using

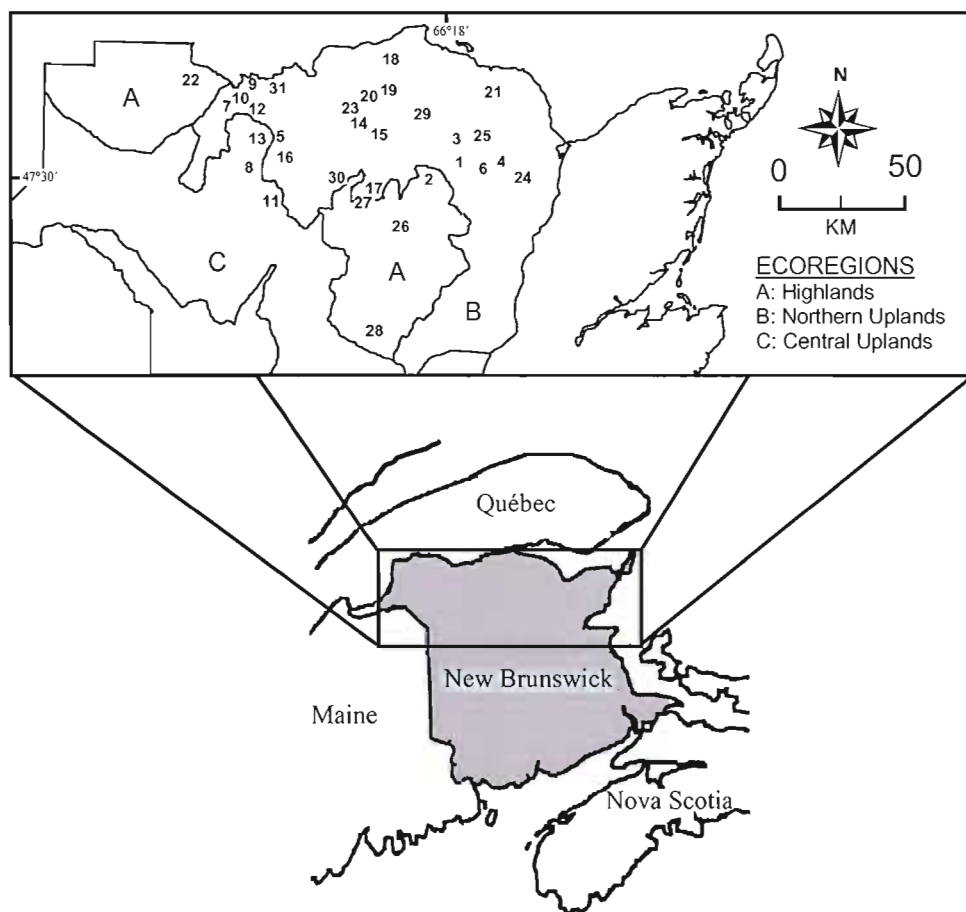


Figure 5.1. Map of study area showing the location of 31 stands sampled in northern New Brunswick.

interpolated weather station data (from the four nearest weather stations) measured from 1970 to 1998 (E. Campbell and J. Régnière, *unpublished data*). Mean annual temperatures ranged from 1.7 to 3.4 °C (average = 2.4°C) and mean annual precipitation from 1010 to 1139 mm (average = 1054 mm). The number of consecutive days without frost ranged among stands from 82 to 121 days (average 104) and minimum winter temperature ranged from -19 to -16 °C. Mean summer precipitation ranged from 466 to 567 mm (average = 500 mm), with the least precipitation occurring in May and June (mean ~ 95 mm).

While forest landscapes of the Highlands are characteristically boreal – balsam fir dominates forests and occurs in stand mixtures with lesser components of white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mill.] BSP), and paper birch (*Betula papyrifera* Marsh.) – the Northern Uplands and Central Uplands are mixedwood landscapes containing large expanses of tolerant hardwoods like sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.) that occupy upper slopes. Balsam fir dominates forests of mid- to low-slopes and these forests contain lesser components of red maple (*Acer rubrum* L.), beech, yellow and paper birch, as well as other conifers like white spruce, white cedar and eastern hemlock (*Tsuga canadensis* [L.] Carrière).

New Brunswick has a 300- to 400-year history of land clearing for agriculture and timber harvesting. Historically, catastrophic fire disturbances were infrequent in this region. Upon European settlement in the area, however, fires became more frequent and have had a more important influence on forest composition (Wein and Moore 1977). Spruce budworm outbreaks have occurred about every 35 years in the study area (Royama 1984). The last outbreak started in 1971 and insecticides were widely applied to minimize the impacts of budworm defoliation.

5.4.2 Stand selection and sampling

The geographic information system software Arc/Info was used to query the New Brunswick Department of Natural Resources forest inventory database for potential sample stands in our study area. The forest inventory database delineates individual stands and assigns them a unique set of attributes including: a stand identifier, stand size (ha), species composition, species percentages, crown closure, maturity class, and soil drainage class. Given that previous studies have shown budworm outbreak impacts (i.e., host defoliation and mortality) vary with stand hardwood content (Bergeron *et al.* 1995; Su *et al.* 1996), we attempted to control for this effect by sampling mature balsam fir-dominated stands (i.e., those with $\geq 80\%$ balsam fir) that contained less than $\leq 20\%$ hardwoods. We first randomly chose among 12 balsam fir-dominated stands (mostly in softwood landscapes) that were previously sampled by MacKinnon and MacLean (2003; 2004). MacKinnon and MacLean initially selected these stands through a stratified random process. The remaining 19 stands sampled were systematically selected through a series of steps. Using ArcInfo queries, we first extracted all stands from the forest inventory database in our study area that was composed of at least 80% balsam fir. For each of these stands, ArcInfo was then used to calculate: i) the proportion of the landscape, within a 1 km radius of the balsam fir stand centroid, that was covered by plantations or recently logged forests, ii) the percentage of the forested landscape, within a 1 km radius of the balsam fir stand, that was covered by stands composed of greater than 75% hardwood species; and iii) distance to the closest road. Among the initial population of balsam fir stands selected, we eliminated those where more than 25% of the surrounding landscape was covered by plantations or recently logged forests. The remaining balsam fir stands were then classified into three groups: i) coniferous landscapes (0-25% hardwood stands), ii) mixedwood landscapes (26-75% hardwood stands); and iii) hardwood landscapes (76-100% hardwood stands). Distance from the nearest road was used to prioritize stands for sampling in each group. A total of 31 stands, representing a gradient in hardwood landscape composition from 2 to 87%, were sampled during 1998, 1999, or 2000.

A 20 x 20 m sampling plot was located at the centroid of each stand. The diameter of all trees (living and dead) taller than >1.3 m was tallied into 5 cm diameter classes. Percent crown cover of all shrubs and herbaceous species in the plot was estimated visually over the entire plot, and in 5 x 5 m subplots when the understory vegetation was particularly dense. In each stand, two increment cores were extracted from opposite sides and at the base (< 30 cm from the germination point) of 10 balsam fir trees. The 10 largest, and presumably oldest, trees closest to the stand centroid were sampled. Basal disks were also collected from up to 10 dead balsam fir.

Using ARC/INFO, the location of each stand sampled was intersected with digitized annual aerial survey maps of forest defoliation and spray blocks. Based on these intersections, we assigned a percent defoliation value to each stand (i.e., the midpoint of defoliation classes assigned during aerial surveys: nil [0-10%]; light [11-30%], moderate [31-70%], and severe [71-100%]. Similarly, the cumulative number of times a stand was sprayed was determined from annual overlays of spray blocks. These data were summarized over all stands.

5.4.3 Chronologies of radial growth

All increment cores and basal disks collected from stands were prepared in the laboratory following standard dendrochronology procedures (Swetnam *et al.* 1985). After sanding and mounting samples, each tree ring on a core was assigned a date (i.e., year of formation) and measured to the nearest 0.001 mm using a Velmex™ Uni Slide Micrometer connected to a computer. The program COFECHA (Holmes 1983) was used to verify dating. Tree-ring series that did not cross-date well with other samples in the stand (i.e., $r < 0.350$ with the stand mean, master chronology) were checked for dating or measurement errors. Series that remained poorly correlated with other samples were eliminated from the dataset of each stand.

The computer program ARSTAN (Cook 1985) was used to produce a standardized chronology of mean annual ring widths for balsam fir in each stand. Raw tree-ring series were standardized through a double detrending method *sensu* Krause and Morin

(1999) (i.e., a negative exponential or straight line, and a cubic spline function with the degree of smoothing fixed at 50% frequency response of 60 years, which conserves 99% of the variation in ringwidth for wavelengths of 1-20 years) to extract variability in individual tree-ring series attributable to tree age/size or vitality and remove shared low frequency trends in annual growths so that shorter periods of budworm-caused growth reductions were highlighted. This detrending process transformed ring widths for individual trees into dimensionless index values. Index values of 1 represented the average growth of a tree over its life-span. Index values greater than 1 indicated above average annual growth while values below 1 indicated below average (i.e., reductions) in annual growth. Index values for each year were averaged over all core samples to produce a standardized mean chronology of annual growth for each stand. This mean chronology was then used to calculate average annual growth reductions (%) for each stand by subtracting the index values for each year from 1 (which represents normal/mean tree growth over its lifespan) and multiplying them by 100. Years with index values above 1 were assigned a percent reduction value of 0. For all stands sampled in northern New Brunswick, the mean percent reduction in radial tree growth was calculated for each year for of the last budworm outbreak in northern New Brunswick (1971 to 1998). Mean annual growth reductions among stands were summarized graphically and compared to defoliation and insecticide spray data. The years in which at least 80% of stands exhibited reductions in growth were selected for subsequent regression analyses, primarily because they were the only years in which the range in growth reduction data was normally distributed (frequent zero values in other years substantially skewed the distributions of growth data).

5.4.4 Data analysis

Multiple linear regression analysis was used to construct models describing relationships between mean balsam fir radial growth reductions in stands (%) (the dependent variable) and the following explanatory variables: i) the percentage of the forest landscape within 1 km of sampled stands that is covered by hardwood-dominated

stands (%); ii) elevation (m); and iii) spray history. A forward selection process was used, with explanatory variables entering the regression model if the F -ratio was greater than 1.0. Elevation was included as an explanatory variable in stepwise regression analyses to account for variation in budworm impacts associated with climatic variations along elevation gradients (largely temperature) and to remove a potential shared gradient in elevation and surrounding forest hardwood content. Regression analyses were run and presented separately for each of the years in which at least 80 percent of stands sampled had growth reductions: 1976-1978, 1982-1984, 1990, 1991 and 1994. Even after data transformations, least squares regression conducted for years where <80% of stands had growth reductions generated unreliable results (i.e., the normality and homogeneity of variance assumptions of least squares regression analysis were not satisfied) and were not presented. In addition to analyses on individual years, regressions were also done for each distinct growth reduction period: 1972-1980, 1981-1985, and 1986-1993. The explanatory variable describing spray history was categorical for analyses on individual years (i.e., sprayed or not sprayed) and continuous for analyses on growth reduction periods (i.e., cumulative number of years sprayed over the period). As the budworm outbreak and insecticide spraying ceased after 1992, spray history was not included as a variable in 1994 analyses.

Before each of these regressions were undertaken, however, we considered the possibility that any statistically significant relationship between host growth reductions during budworm outbreaks and the explanatory variables of interest, particularly forest hardwood content, could be a spurious result of coincidental variation in the explanatory variable with some other unmeasured factor that varied spatially across the study area – climate, for example. To control for this, any potential spatial component of variability in dependant and independent variables was removed through partial regression analysis following Legendre and Legendre (1998). First, we computed a multiple regression of growth reduction onto a spatial matrix of explanatory variables generated by a third-order polynomial of stand coordinates (i.e., latitude and longitude, measured in decimal degrees). A third-order polynomial was chosen as we felt it was of sufficient complexity

to explain any unmeasured, and potentially influential, factors that varied along latitudinal and longitudinal gradients in our study area (*cf.* Legendre and Legendre 1998). The residuals of this multiple regression, which represent variation in budworm-caused growth reductions that remains after spatial gradients in dependent and explanatory variables were removed, were then used to compute subsequent multiple regressions (i.e., partial regressions) that tested the effects of landscape hardwood content, elevation, and insecticide spray history (as described above).

5.5 Results

5.5.1 *Stand characteristics*

Although we extracted stands from the forest inventory database with greater than 80% balsam fir, basal area calculations from tree diameter data collected in each stand indicated that the actual percentage of balsam fir in stands was much more variable, ranging from 24% to 93% (Table 5.1). However, balsam fir was the dominant species in all stands except stands 24 and 18, which had slightly more spruce and white cedar (a non-host softwood species), respectively. The large discrepancy between the percentage of balsam fir indicated on forest inventory polygons and what was calculated from stand survey data is probably due partly to photointerpretation error in distinguishing among conifer species (especially balsam fir and white spruce) on the aerial photographs used to make inventory maps, as well as within-stand variability. We thought that the larger than expected variation in the balsam fir content of stands could generate a significant gradient in growth reductions (with reductions being higher among stands with more balsam fir) that would confound regression analyses used to test the effect of surrounding forest composition. Because of this, we included the percent balsam fir content of stands (i.e., $[(\text{balsam fir basal area, m}^2\text{ha}^{-1} / \text{total tree basal area, m}^2\text{ha}^{-1}) \times 100]$) as a covariable in regression analyses.

Table 5.1. Characteristics of 31 stands sampled in northern New Brunswick.

Stand No.	Elevation (m)	Total tree basal area (m ² /ha)	Stand composition (% basal area)				Surrounding landscape composition (% hardwood forests) [*]	# times sprayed [†]
			BF [‡]	SP	OS	HW		
12	249	39	84	8	0	8	2	20
15	247	47	59	2	24	13	3	17
14	210	50	72	16	5	6	5	15
7	287	56	93	4	0	3	8	17
2	505	43	78	13	0	9	10	22
9	288	39	82	1	0	17	15	19
21	177	40	78	1	4	17	15	15
23	191	49	49	20	32	0	15	15
1	361	31	81	11	0	8	17	18
29	462	47	78	16	0	6	19	9
27	511	47	74	19	0	7	23	19
10	300	43	75	17	0	9	28	18
25	302	37	69	18	0	14	28	20
17	549	45	68	21	2	8	30	18
24	198	66	31	44	2	24	40	13
31	327	51	78	6	0	15	40	17
6	265	34	72	26	0	2	54	14
26	400	33	87	8	0	5	54	12
28	384	44	67	0	0	33	55	10
8	367	36	90	4	0	6	60	10
11	283	58	89	8	0	3	67	17
30	430	40	66	14	0	20	67	13
3	350	43	69	15	0	16	70	17
4	243	52	76	13	0	11	72	7
22	443	30	57	28	0	15	72	12
20	326	34	48	23	28	0	77	3
5	378	50	81	11	0	8	81	7
13	389	46	68	15	0	18	81	5
16	378	42	81	0	0	19	81	7
18	247	41	24	18	27	31	84	3
19	344	33	63	8	3	26	87	8

^{*} Percentage of land covered by hardwood dominated forests within a 1 km radius of the sample stand.

[†] Total number of times sample stand was sprayed with insecticide from 1970 to 1992. Chemical insecticides were used prior to 1988. After 1988, biological insecticides (i.e., *Bacillus thuringiensis*) were applied to most stands. Some stands were sprayed twice in one year.

[‡] BF= Balsam fir; SP= spruce spp. (*Picea glauca*, *P. rubens*, and *P. mariana*); OS = other softwoods (white cedar, white pine); HW = all hardwoods (*Betula* spp., *Acer* spp., *Fagus grandifolia*)

Calculations of stand hardwood content (percentage of total tree basal area) from all stands except stands 24 and 18, which had slightly more spruce and white cedar (a non-host softwood species), respectively. The large discrepancy between the percentage of balsam fir indicated on forest inventory polygons and what was calculated from stand survey data is probably due partly to photointerpretation error in distinguishing among conifer species (especially balsam fir and white spruce) on the aerial photographs used to make inventory maps, as well as within-stand variability. We thought that the larger than expected variation in the balsam fir content of stands could generate a significant gradient in growth reductions (with reductions being higher among stands with more balsam fir) that would confound regression analyses used to test the effect of surrounding forest composition. Because of this, we included the percent balsam fir content of stands (i.e., $[(\text{balsam fir basal area, m}^2\text{ha}^{-1} / \text{total tree basal area, m}^2\text{ha}^{-1}) \times 100]$) as a covariable in regression analyses.

Calculations of stand hardwood content (percentage of total tree basal area) from diameter data collected in each stand corresponded well to the mapped forest inventory data we used to design this study. Hardwood species comprised less than 25 per cent of total tree basal area in all stands except 18, 19 and 28, which had slightly more (Table 5.1). The fact that stand hardwood content corresponded better to mapped forest inventory data than balsam fir content of stands is probably simply because observers can more readily distinguish between hardwood and softwood trees than among softwood species on the aerial photographs used to make the inventory maps. Thus, we are confident that our calculations of landscape hardwood content within 1 km of each stand, which were based on mapped forest inventory data and ranged from 2 to 87 percent (Table 5.1), are reasonably accurate.

Aerial survey data indicated low levels of budworm defoliation (mapped as nil and recorded here as 0-10%, midpoint 5% – MacLean and MacKinnon 1996) from 1960 to 1970 in the stands we sampled (Figure 5.2a). Mean defoliation among stands began to increase in 1971. The highest levels of defoliation occurred in 1973, 1974 and 1975, with the mean defoliation among stands for these years being 41, 65 and 58%,

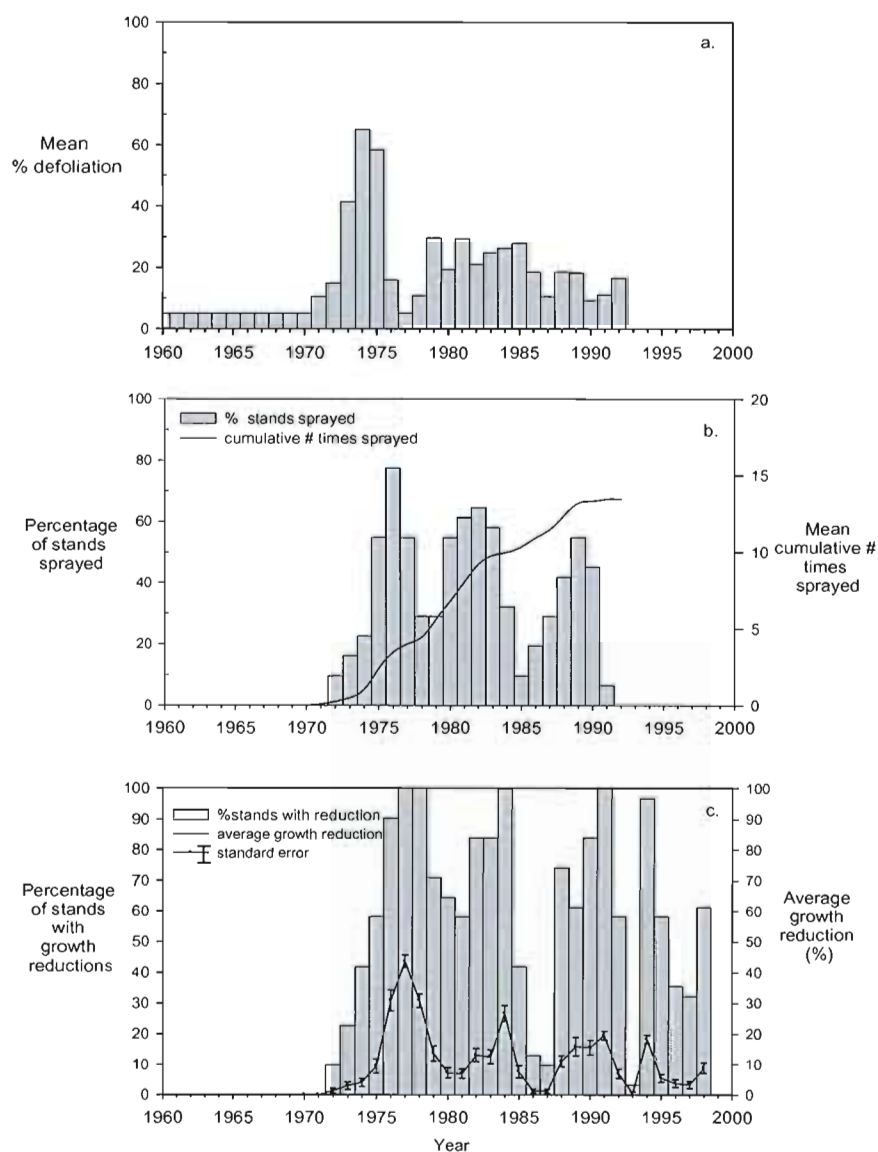


Figure 5.2. a. Mean annual level of defoliation caused by spruce budworm (aerial survey data), b. insecticide spray history over all stands sampled ($N = 31$, the mean cumulative number of times a stand was sprayed by insecticide is indicated by the solid black line), and c. percentage of stands with growth reductions and mean growth reduction (%) in stands from 1970 to 1998.

respectively. Spraying of insecticide to minimize impacts of spruce budworm during the last outbreak began in the early 1970s and was widespread from 1975-1977 when 50-80% of the stands were sprayed each year (Figure 5.2b). As of 1977, these stands had been sprayed, on average, five times. Mean defoliation levels decreased in 1976, 1977, and 1978 but increased again in 1979, hovering between 20 to 30% until 1986, when mean defoliation decreased by another 10%. Extensive spraying occurred again from 1980 to 1983 and in 1989, when at least 50% of the stands were treated. As of 1992, stands were sprayed, on average, 13 times. Stands in hardwood-dominated landscapes tended to be sprayed with insecticides less frequently than those in landscapes of with a lower hardwood forest content ($r = -0.75$; $p < 0.001$) (Table 5.1). Low amounts of dead balsam fir were found in all stands but among stands in landscapes with less hardwood forests, low amounts of dead fir are presumably because frequent insecticide applications reduced budworm populations, and resulting defoliation levels, enough to prevent tree death.

5.5.2 Overall patterns of balsam fir radial growth during the outbreak

Based on the mean standardized chronologies of tree growth developed for each stand, we found that the percentage of stands showing an overall reduction in balsam fir growth varied from 0 to 100% in various years from 1970 to 1998 (Figure 5.3). Although no stands showed reductions in tree growth in 1970 or 1971, the number of stands showing growth reductions steadily increased from 1972 to 1977, and in 1977 and 1978, mean tree growth was reduced in all stands sampled. After 1978, growth reductions occurred in at least 50% of stands sampled over most years, and occurred in at least 90% of stands in 1984, 1991, and 1994.

Initially, the pattern of mean reductions in balsam fir growth (%) was similar to the frequency of growth reductions among stands – mean reductions in growth increased steadily from 1972 until 1977, when all stands had reductions in growth and mean reduction in tree growth over all 31 stands reached a maximum at 44%. The fact that maximum mean defoliation levels occurred in 1974 suggests a 3-year ‘lag’ in growth

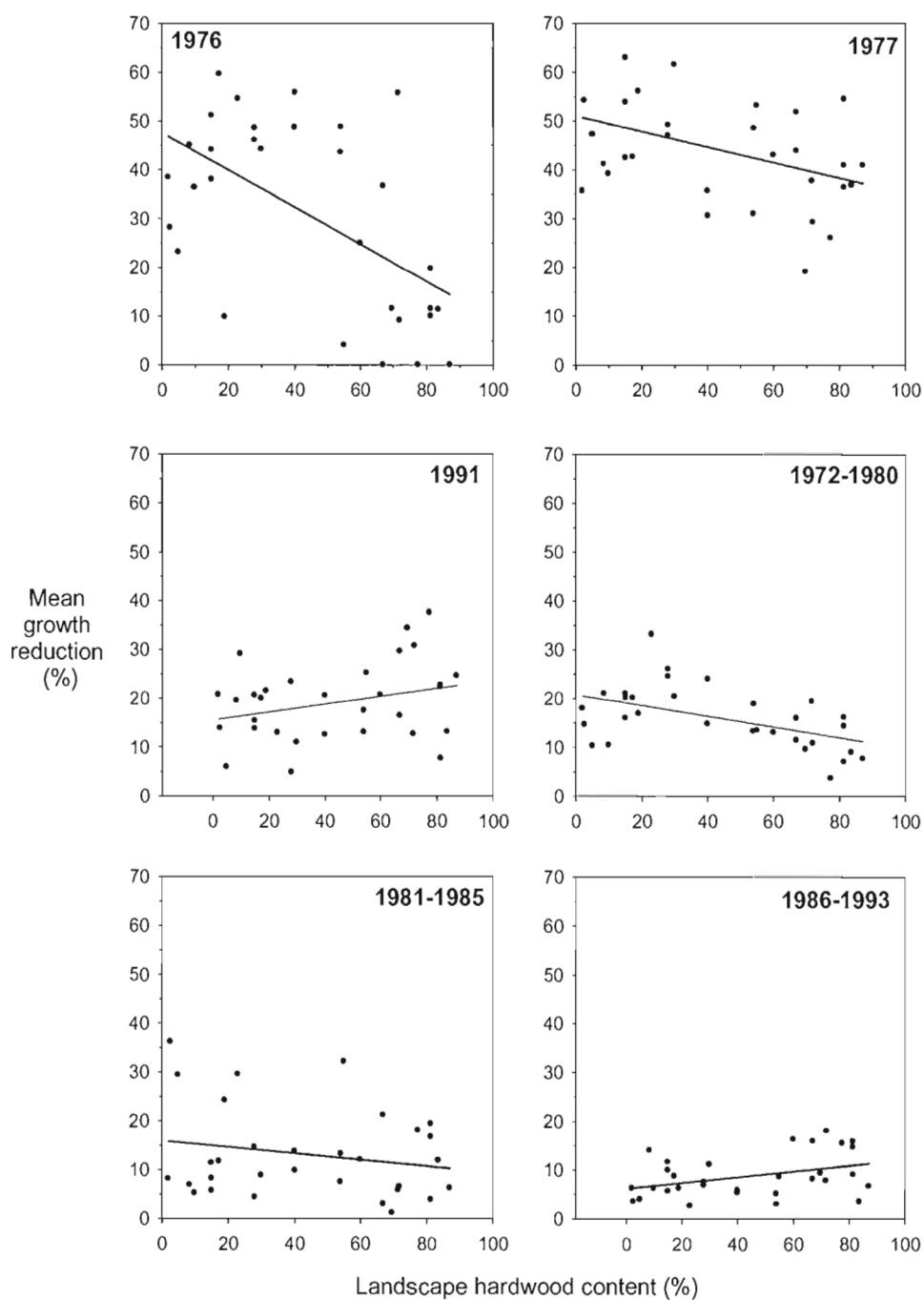


Figure 5.3. Linear relationships between the reduction in radial growth of balsam fir and the hardwood content of forest landscapes within 1 km of each stand sampled ($n = 31$). Results are presented for individual years and time periods that showed significant relationships.

responses to defoliation by spruce budworm during population outbreaks, which really results because defoliation assessed here is for current year foliage only, whereas growth is a function of cumulative defoliation of all age classes of foliage (e.g., Ostaff and MacLean 1995; Erdle and MacLean 1999). Mean growth reductions oscillated following 1977, with peaks in growth reductions occurring again in 1984, 1991 and 1994. Although 90-100% of stands had reduced tree growth during these years, mean growth reductions were about 30 to 50% less than they were in 1977. This may reflect the occurrence of defoliation that includes 'backfeeding' on older age classes of foliage when budworm populations are very high (e.g., Ostaff and MacLean 1995).

5.5.3 Regression analyses

Twelve partial regression models described relationships between residual variation in balsam fir growth reductions (%) among stands and i) the hardwood content of surrounding landscapes, ii) stand elevation, and iii) the history of insecticide spraying (Table 5.2). The hardwood content of surrounding forest landscapes was entered as a variable into all statistically significant (i.e., $P < 0.05$) regression models and explained 12 to 41 per cent of the variation in growth reductions among stands during the last budworm outbreak. There were strong negative relationships between landscape hardwood content and growth reductions during the initial years of the budworm outbreak (i.e., from 1972-1980) (Table 5.2, Figure 5.3) when average growth reductions were most severe and a weak negative relationship in the 1980s when average growth reductions decreased by about 20% (Figure 5.2c). Differences in annual growth reductions among stands were greatest in 1976 (Figure 5.3) – mean growth reductions were about 40% in stands where surrounding landscape hardwood content was <50% and about 20% where landscape hardwood content was >50%. In the following year, growth reductions among stands in hardwood-dominated landscapes rose by about 20%, while those in coniferous-dominated landscapes only increased by 10%. Near the end of the budworm outbreak in northern New Brunswick, when budworm defoliation and growth reductions were comparatively low (Figure 5.2a, c), we found an unexpected

Table 5.2. Summary of stepwise multiple regression analyses accounting for variance in annual growth reductions across all sampled stands ($n = 31$). Analyses were conducted separately for each year in which more than 80% of stands had growth reductions, and then on average reductions over all years for 3 time periods: 1972-1980, 1981-1985, 1986-1993.

Growth reduction (%)	Model statistics				Explanatory variables entered into model			
	Intercept	R^2	MSE	p	Variable*	B	partial r^2	p
1976	9.03	0.46	10.16	0.0008	%hardwood - landscape	-23.02	0.41	0.0010
					% balsam fir - stand	15.67	0.02	0.1963
					elevation	-0.02	0.03	0.2372
1977	6.20	0.24	7.90	0.0204	%hardwood - landscape	-12.42	0.17	0.0094
					insecticide spraying	4.70	0.07	0.1174
1978	4.33	0.05	9.40	0.2476	%hardwood - landscape	-6.13	0.05	0.2476
1972-1980	4.80	0.20	4.53	0.0110	%hardwood	-6.79	0.20	0.0110
1982	10.49	0.05	8.07	0.2239	% balsam fir - stand	-10.42	0.05	0.2239
1983	10.18	0.12	8.74	0.1602	elevation	-0.02	0.07	0.1682
					insecticide spraying	-4.11	0.05	0.2067
1984					No variables entered			
1981-1985	14.82	0.19	6.35	0.0514	Cumulative no. yrs sprayed	-0.85	0.06	0.0238
					%hardwood	-8.84	0.13	0.0444
1990	-4.22	0.03	10.79	0.3240	%hardwood	5.98	0.03	0.3240
1991	-5.02	0.12	6.50	0.0574	%hardwood	7.11	0.12	0.0574
1994	-6.05	0.05	4.94	0.2513	% balsam fir - stand	6.00	0.05	0.2513
1986-1993	-3.17	0.19	3.16	0.0155	%hardwood	4.49	0.19	0.0155

* to improve residual normality and reduce heteroscedasticity of residual variance, %hardwood content and % basal area of balsam fir were transformed using the following function: $\arcsin(\sqrt{x/100})$. Explanatory variables are listed in the order by which they were entered into models.

weak positive relationship between balsam fir growth reductions and landscape hardwood content (Table 5.2, Figure 5.3). While this relationship was of borderline statistical significance for 1991, the relationship was stronger for the period 1986-1993 (Table 5.2).

Relationships between growth reductions and stand elevation or insecticide spray history were weak (Table 5.2). Elevation was entered into the 1976 and 1983 regression models, but did not explain a statistically significant percentage of the variation in growth reductions among stands. Similarly, although the effect of insecticide spraying was entered into regression models for 1977 and 1983, it also did not explain a significant proportion of the variation in growth reductions among stands for these years. However, there was a statistically significant, albeit somewhat weak, negative relationship between the cumulative number of times a stand was sprayed up to 1985 and average growth reductions over the period spanning 1981-1985 (Table 5.2, Figure 5.3). By 1985, all stands had been sprayed at least three times and about 60% of stands had been sprayed more than 10 times. Growth reductions were, on average, 6 % less severe in stands sprayed more than 10 times.

5.6 Discussion

We examined variations in the impact that spruce budworm outbreaks have on balsam fir/spruce-dominated stands in northern New Brunswick. Impact can be evaluated using various measures over various scales. Whereas we quantified impact by measuring the degree to which balsam fir radial growth was reduced in stands during spruce budworm outbreaks, others have quantified impact by measuring host defoliation levels among species (Nealis and Régnière 2004), in stands (MacKinnon and MacLean 2003) and over landscapes (Gray *et al.* 2000; Candau and Fleming 2005). Host mortality levels have also been used to measure outbreak impacts (MacLean and Ostaff 1989; Bergeron *et al.* 1995). Of course, variation in impact of budworm outbreaks on hosts does not always reflect variation in budworm population densities, as other have

shown (Lysyk 1990; Nealis and Régnière 2004). The sometimes weak, or non-linear, relationship between outbreak impact and budworm abundance is because impact is not only influenced by budworm population densities but also by the ability of hosts to withstand effects of a given population level of these defoliators. In many cases, therefore, budworm impacts on forests result from an interaction between these factors. While information about budworm population dynamics must form the basis of managing outbreaks impacts over the long-term, describing and quantifying patterns of budworm impact is often of more immediate and practical relevance to forest managers as it provides a means to identify stands that are most vulnerable to outbreaks and to target management strategies (e.g., adjustments of harvest scheduling, insecticide applications, etc.) accordingly.

We found a significant negative relationship between the hardwood content of surrounding forest landscapes (%) and mean balsam fir radial growth reductions (%) during the initial years of the last spruce budworm outbreak in northern New Brunswick. As forest landscape hardwood content increased, mean growth reductions in balsam fir/spruce-dominated stands decreased. This finding is consistent with a previous stand-level study in New Brunswick (Su *et al.* 1996), where defoliation caused by budworm outbreaks was much less in stands mixed with hardwood species than in host-dominated stands. It also supports a long history of studies indicating that forest composition has significant influence on the impact of budworm outbreaks (Fauss and Pierce 1969; MacLean 1980; Bergeron *et al.* 1995; MacKinnon and MacLean 2003). On the other hand, our finding seems contradicted by another study in New Brunswick that found no statistically significant differences in balsam fir or spruce growth reductions among stands in softwood or mixedwood landscapes (MacKinnon and MacLean 2004). However, this study suffers from the shortcoming of not having removed the potentially confounding spatial component to budworm-caused growth reductions and forest composition.

Several hypotheses can be proposed to explain why host growth reductions of balsam fir were less severe in stands surrounded by hardwood forests. Initial

populations in these stands may have been lower because fir stands isolated in hardwood landscapes are simply harder for dispersing moths to find. However, in a Quebec study Cappuccino *et al.* (1998) found that moth densities did not significantly differ among balsam fir stands isolated by hardwood forests and contiguous tracts of balsam fir forests. Thus, stand isolation is an unlikely explanation for our findings. High levels of competition in small stands isolated by hardwood forests could contribute to significant losses of first- and second-instar larvae during dispersal to other hosts (Kemp and Simmons 1978). While the stands we sampled were dominated by host trees, balsam fir or spruce, dispersal losses could be a significant contributing factor among isolated stands if stand edge to area ratio is high (Roland 1993; Kouki *et al.* 1997). A favoured explanation for lower budworm impacts in balsam fir/spruce stands surrounded by hardwood forests is that they contain more abundant and a more diverse complex of budworm natural enemies. Cappuccino *et al.* (1998) found that tachinid parasitism of larvae and ichneumonid parasitism of pupae were greater in balsam fir stands isolated by hardwood forests than in expansive tracts of balsam fir. Similarly, Quayle *et al.* (2003) found parasitism of eggs by a hymenopteran species was greater in balsam fir stands than in stands mixed with hardwood species. More abundant nectar sources and alternate hosts associated with hardwoods likely explain the higher parasitoid densities (Simmons *et al.* 1975; Houseweart *et al.* 1984) that help to suppress budworm populations. Larval predation by a potentially more diverse community of birds at forest edges and in mixedwoods may also be a contributing factor (Crawford and Jennings 1989; Drapeau *et al.* 2000). Another explanation for lower growth reductions in stands of hardwood landscapes may be related to site conditions.

To reduce the level of damage caused by the last spruce budworm outbreak in New Brunswick, large insecticide spray programs were undertaken from 1972 to 1993. We found that spray history was generally a weak and inconsistent predictor of the degree to which balsam fir growth was reduced during budworm outbreaks. The lack of spray effects in individual years undoubtedly reflects the fact that host growth reductions in a given year are more strongly related to the cumulative effects of defoliation, over a

number of years on all ages of foliage, than the level defoliation that occurs in any given year (Erdle and MacLean 1999). Since spraying against budworm generally only influences current-year defoliation, it perhaps is not surprising that we found no effect during the individual years tested. The fact that cumulative defoliation levels, rather than to defoliation in any one particular year, more strongly affect growth reductions is emphasized by our finding that host growth reductions from 1981 to 1985 tended to be less severe among stands that had been sprayed more often. However, cumulative spraying effects were inconsistent, with no effect observed during the other two growth periods tested: 1972-1980 and 1986-1993. Weak relationships between budworm impact levels and spraying are reported throughout the literature. MacLean *et al.* (1984) found little difference in volume losses among insecticide-treated and untreated spruce, and spraying seems to have little influence on large-scale patterns of budworm defoliation (Fleming *et al.* 1984; Hardy *et al.* 1986). We suspect that spatial scale of analysis, varying local factors that affect budworm densities (or host vulnerability), as well as spraying methods, intensity and varying efficacy, may all confound the ability to detect relationships between growth reductions and insecticide spray history, especially with a relatively small number of samples. It is also important to note that insecticide spraying in New Brunswick has been designed to prevent tree mortality rather than to minimize growth reduction (MacLean *et al.* 1984).

An unexpected finding of this study was the temporal trend in the influence of landscape hardwood content on balsam fir growth reductions. Su *et al.* (1996) recognized the potentially confounding effect that outbreak year may have on forest composition effects when their regression models indicated that stand hardwood content explained progressively less variation in defoliation levels among stands over time, in the years toward the end of the budworm outbreak (1989-1993). This temporal trend is consistent with our regression results from 1976 to 1985. However, when Su *et al.* (1996) followed their regression analyses with a test for a hardwood content-outbreak year interaction effect and found it to be insignificant, they proposed that increasing forest hardwood content has same proportional decrease in budworm impacts, regardless

of changes in budworm population levels over time. Our results don't support this hypothesis. When average defoliation levels decreased substantially from the early 1980s onward, presumably a reflection of low budworm densities resulting from the combined effects of cumulative spraying and natural drivers of decreasing population trends, forest hardwood content explained little to no variance in growth reductions among stands in the 1980s. When budworm population densities are low, it is possible that parasitoids are sufficiently abundant in all forests to dilute any spatial variation in budworm impacts that are mediated by forest hardwood content. This does not preclude the idea that rates of parasitism vary with forest hardwood content, even when budworm populations are low (i.e., at endemic levels), as two studies in Quebec have shown (Cappuccino *et al.* 1998; Quayle *et al.* 2003). It simply suggests that impacts related to hardwood content, can no longer be detected when populations are low and causing little damage. A potentially interesting extension to this study might be to examine how parasitism rates vary through the course of an outbreak in relation forest hardwood content. The positive relationship between growth reductions and surrounding forest hardwood content in the late 1980s and early 1990s is a more curious finding that may be partly related to a greater, or more rapid reduction in budworm population densities among stands of fir dominated landscapes that were sprayed more frequently.

5.7 Conclusions

This study showed that surrounding forest hardwood content significantly influences the severity of growth reductions in mature balsam fir-spruce stands. This finding lends support to the “silvicultural hypothesis”, which states that forest management activities altering forest composition could be used to minimize budworm impacts. What makes this study stand apart from others that have examined relationships between forest composition and outbreak impacts, is that it measures budworm impacts on individual trees (i.e. growth loss during budworm outbreaks), rather than using some landscape-level spatially integrated measure of damage extent.

Because host growth losses during budworm outbreaks directly reflect budworm population densities, this study forms a strong basis from which to make inferences about the effects of forest composition on local-scale budworm population dynamics. Of particular significance is the fact that our study shows forest composition has an active effect on budworm populations, which is mediated through differences in parasitism rates related to forest hardwood content, and not just a passive effect of increasing amounts of host available for defoliation (e.g., Blais 1983). Distinguishing between active and passive effects of forest composition on budworm outbreak impacts has significant implications for how foresters might alter forest landscape composition to minimize future budworm impacts. Increasing hardwood content may yield proportionately greater rewards.

Forest managers are interested in cost-effective ways to reduce spruce budworm outbreak impacts on timber supplies. While spraying insecticides has been used extensively throughout New Brunswick in the past, attaining protection objectives through widespread application of biological insecticides will be costly. We suggest that increasing the hardwood content of managed forest landscapes could help to reduce the impact of budworm outbreaks. However, forest management plans designed to minimize budworm outbreak impacts, should combine several strategies, like planting of non-host softwood species, harvest scheduling and silviculture (e.g., stand thinning), and judicious use of insecticides, with ways to increase forest hardwood content. Additionally, the effects of surrounding hardwood content should be incorporated into decision support tools that predict stand vulnerability, such as the Spruce Budworm Decision Support System (MacLean *et al.* 2001; 2002). More accurate predictions of stand vulnerability will help to target specific management strategies.

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Liens : Dans l'article II nous avons examiné comment les diminutions de croissance radiale des hôtes dans peuplements matures au Québec ont variées avec le pourcentage des peuplements feuillus dans la mosaïque forestière. Dans le prochain article, nous avons incorporé ces informations sur la variabilité de la sévérité des épidémies dans les outils décisionnels permettant de prédire les impacts des épidémies de TBE à venir. Ces travaux de modélisation, implémentés pour la Forêt d'Enseignement et de Recherche du Lac Duparquet en Abitibi, montrent une estimation des pertes potentielles de volume ligneux (en m^3/ha) pour 7 scénarios d'épidémies de la TBE.

6 ARTICLE V - INCORPORATING FOREST COMPOSITION EFFECTS ON DEFOLIATION INTO AN IMPLEMENTATION OF THE SPRUCE BUDWORM DECISION SUPPORT SYSTEM IN NORTHWESTERN QUEBEC

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6.1 Résumé

Un Système d'Aide à la Décision (SAD-TBE) traitant des impacts la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) a été utilisé pour estimer les volumes de bois qui seraient perdus suite à une future épidémie de tordeuse des bourgeons de l'épinette (TBE) dans la région nord-ouest du Québec. Les résultats de différents scénarios (11) ont été comparés afin d'évaluer la nécessité d'utiliser des modèles de défoliations annuelles qui : i) sont spécifiques à la région géographique où le SAD-TBE est mis en œuvre et ii) incorporent les effets de composition forestière (abondance de feuillus) sur la sévérité des épidémies de TBE dans peuplements. Les scénarios incorporent 17 modèles de défoliation annuelles qui ont été dérivées des données historiques sur les niveaux de peuplements de TBE et des données sur les impacts des épidémies. Les modèles représentant des épidémies 'modérées' avait 6 à 7 ans de la défoliation annuelle au-dessus le but d'aménagement de 40% défoliation annuelle. Les modèles représentant des épidémies sévères avaient 9 à 12 ans au-dessus ce seuil. Parmi les modèles de défoliation représentant les épidémies 'modérées', la défoliation annuelle maximum pour les modèles dérivées des données du Nouveau-Brunswick était 20% plus haut que la défoliation maximum pour les patrons dérivés des données du Québec. Les pertes de sapins et d'épinettes estimées à partir de ces scénarios ont varié de ~18 000 à ~92 000 m³ pour tous les scénarios d'épidémies modérées et de ~64 000 à ~148 000 m³ pour des scénarios d'épidémies sévères. Les variations dans les pertes estimées pourraient refléter des différences régionales dans la sévérité de la défoliation bien que cette tendance puisse être masquée par les types de données desquelles les modèles de prédiction ont été dérivés (données sur la population de TBE, points de cartes de défoliation effectuées à la main, patrons de diminution de croissance durant les épidémies). Par ailleurs, notre résultats démontrent clairement que les pertes estimées étaient surestimé par 23% à 27% quand les modèles de défoliation ne tenaient pas compte de l'abondance des feuillus dans le paysage entourant le peuplement. Les implantations courantes du SAD TBE ont appliquées seulement un modèle de la défoliation à tous les peuplements susceptibles dans un paysage aménagé. Afin d'obtenir l'estime 'meilleur' de futures pertes au cause des épidémies, nous recommandons que les implantations futures du SAD TBE, appliquent plusieurs modèles de la défoliation à un paysage ainsi que les impacts d'une épidémie dans chaque peuplement soit réfléchissant l'abondance de feuilles dans le peuplement et dans le paysage environnant.

Mots-clés: système d'aide à la décision, dommages par les insectes, modèles, scénarios, tordeuse des bourgeons de l'épinette

6.2 Abstract

The Spruce Budworm Decision Support System (SBW DSS) was used to estimate potential volume losses caused by a future spruce budworm (*Choristoneura fumiferana* [Clem.]) outbreak in northwestern Quebec. The outcomes of 11 outbreak scenarios were compared to evaluate the implications of incorporating annual defoliation forecasts that: i) are specific to the geographic region within which the SBW DSS is being implemented, and ii) incorporate the effects of forest hardwood content outbreak severity. The scenarios incorporate 17 annual defoliation forecasts that were derived from historical outbreak data on budworm population levels and budworm impacts. While forecasts representing “normal” outbreaks had 6-7 years of annual defoliation above the forest management target of 40% annual defoliation, “severe” outbreaks had 9-12 years above this threshold. Among defoliation forecasts representing “normal” outbreaks, maximum annual defoliation for the forecast derived from New Brunswick data was 20% higher than maximum defoliation for the forecasts derived from Quebec data. Overall 11 outbreak scenarios were applied to the test landbase; projected total volume losses of balsam fir (*Abies balsamea* [L.] Mill) and spruce (*Picea* spp.) ranged from ~19 000 to 92 000 m³ of under “normal” outbreak scenarios, and from 64 303 to 148 000 m³ under “severe” outbreak scenarios. While this variation in projected volume losses could be due to regional variations in defoliation patterns, any ability to detect such a trend was confounded by the different data sources and methods used to derive defoliation forecasts. On the other hand, our results demonstrated clearly that projected volume losses could be overestimated by 23 to 27% if defoliation forecasts used by the SBW DSS are not adjusted to account for the effect of forest hardwood content on stand vulnerability to budworm outbreaks. To date, implementations of the SBW DSS have applied a single defoliation pattern to all susceptible stands in a managed landscape. To obtain the “best” estimate of future volume losses, we recommend that future SBW DSS implementations apply multiple defoliation patterns to a landscape so that the impacts of an outbreak in each stand are reflective of stand and surrounding forest hardwood content.

Keywords: decision support tools; insect damage; scenario modelling; spruce budworm

6.3 Introduction

Periodic outbreaks of the spruce budworm (*Choristoneura fumiferana* [Clem.]) (Lepidoptera: Tortricidae) occur throughout boreal and mixedwood forests of North America. Repeated annual defoliation during budworm outbreaks causes significant reductions in balsam fir (*Abies balsamea* [L.] Mill.) growth and spruce (*Picea* spp.) and frequently kills host trees over vast geographic areas (Hardy *et al.* 1986). In eastern Canada, three major spruce budworm outbreaks have occurred over the last century, starting around 1908, 1930, and 1970 and lasting about 10 years (Brown 1970; Kettela 1983; Simpson and Coy 1999). While these periodic natural forest disturbances play an important ecological role in restructuring forests and recycling nutrients, they also reduce timber supplies and generate substantial socio-economic losses. From 17-22% of Canada's annual timber supply was lost to the spruce budworm between 1977 and 1987 (Sterner and Davidson 1982; Power 1991; National Forestry Database 1995).

Spruce budworm outbreaks cannot be prevented (Royama 1984; Royama *et al.* 2005) but forest management could be used to reduce their future impacts (MacLean 1996; MacLean *et al.* 2001). To help foresters make decisions about managing damage caused by spruce budworm outbreaks, the Canadian Forest Service developed the Spruce Budworm Decision Support System (SBW DSS) (MacLean and Porter 1994; 1995). The SBW DSS is based upon a scenario-planning approach – a manner of strategic planning that generates a wide array of possible future outcomes, or hypothetical “what if” scenarios (Schoemaker 1995). In other words, the SBW DSS permits forest managers to forecast and compare the consequences of varying budworm disturbance regimes or alternative management actions to limit budworm damage. It uses: i) mapped forest inventory data to describe the current landbase (MacLean *et al.* 2000); ii) aerial surveys and field data that monitor budworm population levels (MacLean *et al.* 2000); iii) models predicting stand vulnerability and budworm outbreak dynamics (Royama *et al.* 1984; MacLean *et al.* 2000); iv) a stand dynamics model (MacLean 1996; Erdle and MacLean 1999) and a regional timber supply model that

incorporates stand- and forest-level effects of defoliation into forecasts of future forest inventories; and v) ARC/INFO and ArcView geographic information systems to manipulate spatial data, generate maps of potential budworm-caused timber volume losses (m^3/ha), and identify the stands most vulnerable to outbreaks. The SBW DSS has been implemented operationally throughout New Brunswick (MacLean *et al.* 2002) and Saskatchewan and on test landbases in Alberta, Ontario, and Quebec. While the focus of this decision support system has been to project the consequences of budworm outbreaks on timber supplies, it has also been used to assess the potential effects of budworm outbreaks on other forest values (MacLean *et al.* 2000).

Implementing the SBW DSS requires forecasts of annual defoliation levels that will occur during a future budworm outbreak. This is currently estimated by incorporating annual defoliation patterns observed during past outbreaks into a growth and yield model – STAMAN. Annual defoliation levels are converted to cumulative defoliation and empirical relationships between cumulative defoliation and tree growth and mortality are used to calculate stand volume losses (MacLean 1996; Erdle and MacLean 1999; MacLean *et al.* 2001). To date, the SBW DSS has been implemented across Canada using two generalized defoliation patterns – representing a “normal” and a “severe” budworm outbreak, respectively – that were derived from historical studies of budworm population cycles in New Brunswick (Royama 1984; MacLean *et al.* 2001). The system has used only one of these defoliation patterns at a time and applied the same one to all susceptible stands over the landbase. While designers of the SBW DSS recognize that there is likely considerable variability in the defoliation patterns that describe “normal” and “severe” outbreaks (MacLean 1996; MacLean *et al.* 2000), this variability has not yet been incorporated into SBW DSS implementations, largely due to limited data about how defoliation patterns vary regionally and from stand to stand. However, the results of several recent studies make important contributions to resolving this issue.

Large-scale regional differences in defoliation patterns caused by budworm outbreaks have recently been investigated. Twenty-seven distinct patterns describe the temporal and spatial variation in defoliation over eastern Canada (Gray *et al.* 2000; Gray

and MacKinnon 2006). Candau and Fleming (2005) investigated ecological factors responsible for generating temporal and spatial variability in defoliation patterns in Ontario; they found regional differences were significantly related to climate and forest composition.

Within a single geographic region, where climate is relatively homogeneous, variations in budworm-caused defoliation patterns have also been related to local stand conditions. MacKinnon and MacLean (2003) found that average annual defoliation levels in spruce-fir dominated stands were more severe on moist/rich sites than wet/poor sites. Variations in stand age and tree species are also related to differences in defoliation patterns, with annual defoliation levels increasing among older stands with more abundant hosts (MacLean 1980; Nealis and Régnière 2004; MacKinnon and MacLean 2003) and decreasing, on the other hand, as the hardwood content of stands increases (Su *et al.* 1996). An increasing amount of evidence suggests that the spatial context of stands may also play an important role. In New Brunswick, MacKinnon and MacLean (2003) found that average annual defoliation of white spruce (*Picea glauca*, [Moench] Voss) in softwood landscapes was 11% greater than in those of mixedwood landscapes. In Ontario, Kouki *et al.* (1997) found that host defoliation caused by jack pine budworm (*Pinus banksiana* Lamb.) was more severe among old stands when they were adjacent to younger, more open forests. To date, the most intensive studies on the effects of stand spatial context describe the severity budworm-caused radial growth reductions in relation to the hardwood content of surrounding forest landscapes (Chapter 2: Article I, and Chapter 3: Article II). Growth reductions of balsam fir in spruce-fir dominated stands were more intense and occurred over a longer period of time as the hardwood content of surrounding forests decreased. Given a strong linear relationship between host radial growth and defoliation by budworm (%) (Erdle and MacLean 1999), we expect defoliation patterns to vary similarly with surrounding forest hardwood content.

The overall goal of this work was to incorporate new information about the variation in budworm defoliation patterns into an implementation of the SBW DSS. We

specifically wanted to incorporate information about how defoliation patterns vary with forest hardwood content, especially the hardwood content of surrounding landscapes (i.e., stand spatial context). Given the above, the SBW DSS was implemented for a test landbase in northwestern Quebec, a mixedwood boreal forest landscape where a large amount of data on surrounding forest hardwood effects had already been collected (see chapter 3: Article II). By comparing among model run results that exclude and include hardwood effects, it was our intention to quantify the degree to which incorporating forest hardwood effects into the SBW DSS reduced projected future budworm-caused volume losses (m^3). Similarly, by comparing projected volume losses using defoliation patterns from Quebec and New Brunswick, we evaluated the appropriateness of using the New Brunswick defoliation patterns for implementing the SBW DSS in Quebec.

6.4 Methods

6.4.1. The Test Landbase

The SBW DSS was implemented for the Lake Duparquet Research and Teaching Forest (LDTRF), which is situated at the southern limit of the boreal forest near the Quebec/Ontario border (Fig. 6.1). The LDTRF was created under the Quebec Forest Act in 1995 and the Ministry of Natural Resources has entrusted its management to the University of Quebec at Montreal and the University of Quebec in Abitibi-Témiscamingue. The LDTRF test landbase (8 045 ha) represents mixedwood forest landscapes typical of the southern boreal forest (Bergeron and Bouchard 1983; Bergeron 2000). With most stands having greater than 9% fir-spruce content, 81% of the forest land in the LDTRF is susceptible to budworm outbreaks (Table 6.1). Most of the LDTRF is covered by: i) balsam fir- and/or spruce-dominated stands mixed with hardwoods, predominantly paper birch, *Betula papyrifera*, (Table 6.1, Fig. 6.1) and, ii) hardwood dominated stands (i.e., trembling aspen, *Populus tremuloides* Michx., or paper birch-dominated stands) mixed with balsam fir and/or spruce (Table 6.1, Fig. 6.1). Nearly pure balsam fir and/or spruce stands (80-100% spruce and/or fir) are much less

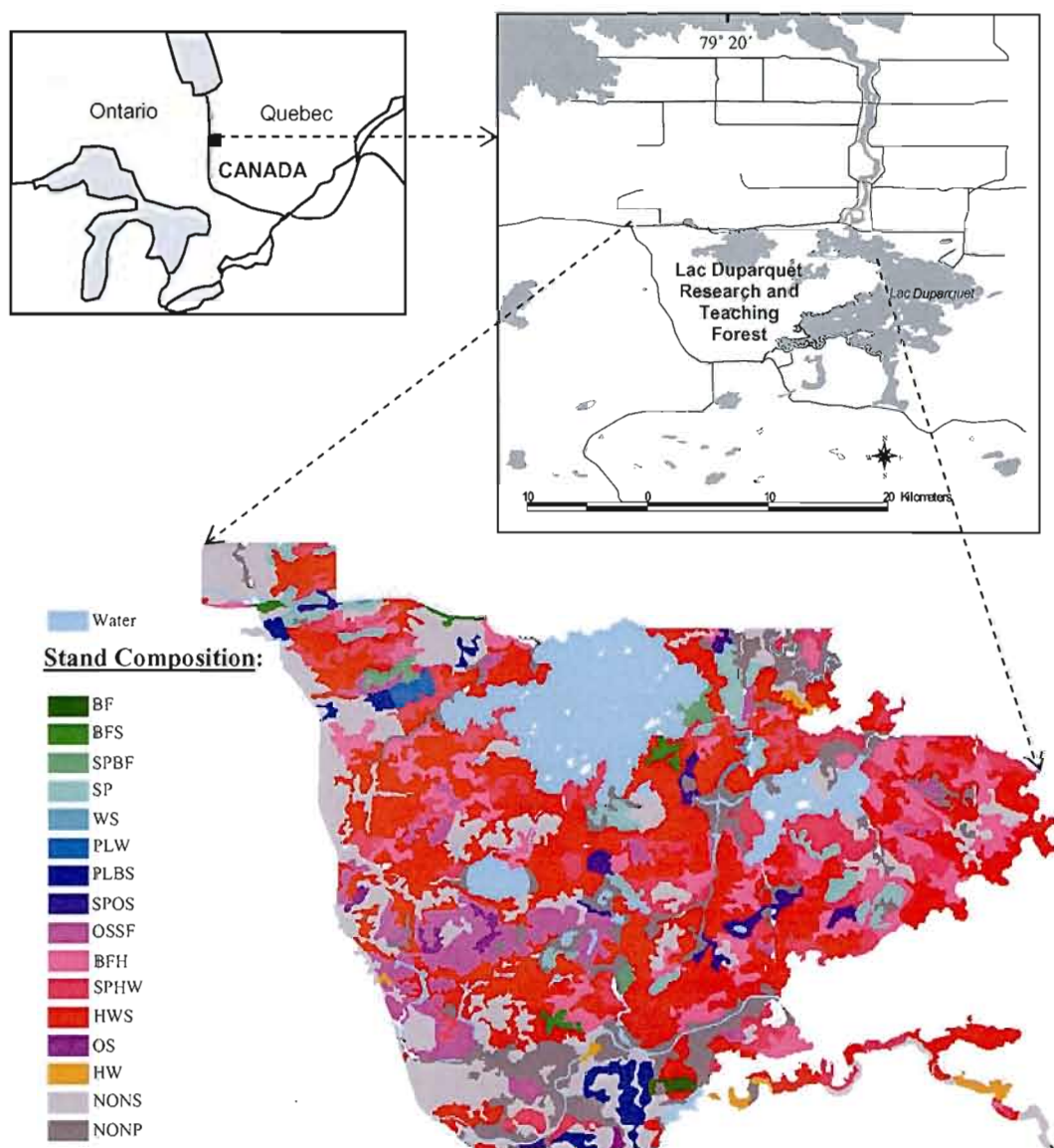


Figure 6.1. Map showing the location of the test landbase, at Lac Duparquet in northwestern Quebec and stand composition. Stand composition codes are as follows: BF - $\geq 80\%$ balsam fir (*Abies balsamea*); BFS - $\geq 80\%$ balsam fir and spruce, BF \geq SP; SPBF - $\geq 80\%$ balsam fir and spruce, SP \geq BF; WS - white spruce (*Picea glauca*), SP - spruce spp. (*Picea* spp.), PLW - white spruce plantation, PLBS - black spruce (*Picea mariana*) plantation, OS - other non-host softwood species (e.g., *Pinus banksiana* and *Thuja occidentalis*), HW - hardwood species, NONS - non-susceptible forest, NONP - non-productive forest land.

Table 6.1. Land cover classification for the Lac Duparquet Research and Teaching Forest (LDTRF) (8045 ha) of northwestern Quebec. Among productive forest lands, stand types are classified according to species composition and their susceptibility to spruce budworm outbreaks. Following MacLean *et al.* (2001), stands with less than 9% spruce-fir are considered non-susceptible.

Stand type	Stand type code ^a	Spruce-fir content (%)	Tree species composition (%)	LDTRF area covered (%)
A. Productive forest: natural stands				
Balsam fir	BF	80-100	BF \geq 80	0.2
Fir-spruce	BFSP		BF \geq SP	0.5
Spruce-fir	SPBF		SP \geq BF	0.6
Spruce	SP		SP \geq 80	2.9
White spruce	WS		WS \geq 80	0.2
Total				4.4
Fir – hardwood	BFHW	50-79	BF \geq SP, HW \geq OS	8.4
Spruce – hardwood	SPHW		BF < SP, HW < OS	9.3
Spruce – other softwood	SPOS		BF < SP, HW \geq OS	1.2
Total				19.0
Hardwood	HW	10-49	HW \geq 80	0.6
Other softwood	OS		OS \geq 80	0.4
Hardwood – spruce or fir	HWSF		HW \geq OS	30.0
Other softwood – spruce or fir	OSSF		HW < OS	5.5
Total				36.9
Non-susceptible stands	NONS	0-9	SP or BF <10	15.0
B. Productive forest: silviculturally treated stands				
Planted white spruce	PLWS		WS \geq 80	0.3
Planted black spruce	PLBS		BF < BS, BS \geq 80	1.5
Total				1.9
C. Non-productive land				
Non-productive vegetated lands	NONP			22.0
Open water	Water			0.9
				22.9

^a BF=balsam fir, BS=black spruce SP=spruce (red/black spruce), WS=white spruce, HW=hardwoods, OS=other softwoods, PL=planted, NONS=with non-susceptible to budworm outbreaks, NONP=non-productive vegetated lands (predominantly wetlands dominated by Alder, tamarack, black spruce, and white cedar but also rocky outcrops with black spruce or white cedar).

abundant (Table 6.1, Fig. 6.1), as are stands with $\geq 80\%$ hardwoods or $\geq 80\%$ other non-host softwood species like jack pine, *Pinus banksiana* Lamb., or eastern white cedar, *Thuja occidentalis* L., (Table 6.1, Fig. 6.1). Stands of fir-spruce mixed with other softwoods (mostly jack pine) are somewhat more abundant than nearly pure fir-spruce stands (Table 6.1, Fig. 6.1). Plantations of black spruce, *Picea mariana* [Mill.] B.S.P., and white spruce, *Picea glauca* (Moench) Voss, cover a small part of the LDTRF (Table 6.1, Fig. 6.1). About 22% of the LDTRF is covered by non-productive vegetated lands – while some of these are dry, rocky outcrops with black spruce, red pine, *Pinus resinosa* Ait., and jack pine or eastern white cedar, most are wet sites (bogs and floodplains dominated black spruce; white cedar; tamarack, *Larix laricina* [Du Roi]K. Koch.); black ash, *Fraxinus nigra* Marsh.; American elm, *Ulmus Americana* L., and shrubby species like Alder, *Alnus* spp.

The LDTRF has been subject to periodic spruce budworm outbreaks. While aerial surveys for this region indicate that spruce budworm outbreaks occurred in the LDTRF from 1940 to 1950 and again from 1971 to 1985, tree ring records indicate outbreaks have occurred about every 32 years for at least the last two centuries (Morin *et al.* 1993; see Chapter 2: Article I). Spruce budworm population sampling has indicated that an outbreak may be beginning again in parts of Quebec. While this outbreak has not yet reached the LDTRF, it is expected to occur in the next few years.

6.4.2 Forecasts of Annual Defoliation

Seventeen forecasted defoliation patterns were used to evaluate the implications of incorporating regional variability and forest composition effects into SBW DSS projections of future budworm outbreak impacts in the LDTRF. These forecasts were estimated from historical annual defoliation data derived from three sources:

- i. **Published literature** – Defoliation patterns representing “normal” and “severe” budworm outbreaks in New Brunswick (MacLean *et al.* 2001) were derived from historical data on budworm population cycles in New Brunswick (Royama 1984;

Deloitte and Touche Management Consultants 1991; Erdle and MacLean 1999). The defoliation pattern representing a “severe” outbreak in Abitibi region of Québec (defoliation pattern #25, Gray *et al.* 2000) was calculated from aerial survey maps of defoliation.

ii. Aerial sketch maps of defoliation in the vicinity of the LDTRF – A GIS

intersection of 31 systematically selected points (located at the centroid of spruce–fir-dominated stands within ~ 20 km radius of the LDTRF; see Chapter 3: Article II) and aerial sketch mapped defoliation polygons were used to derive two defoliation patterns. For each point-polygon intersection, average tree defoliation was described in three categories: nil (0% defoliation), light (1-35% defoliation) and moderate-severe (>35% defoliation). The mid-point of the light and moderate-severe defoliation classes were averaged over all stands to represent what we have termed a “normal” outbreak, and the maximum of each category was averaged over all stands to represent what we have termed a “severe” outbreak. Although the hardwood content of landscapes surrounding the point locations varied from 1-83%, we were unable to detect differences in annual defoliation patterns by landscape type due to the coarseness of the mapped defoliation data (i.e., large defoliation polygons covered many point locations and defoliation classes were broad). As such, we relied on radial growth data collected from individual stands to assess forest composition effects.

iii. Host radial growth data collected for the LDTRF – Annual defoliation patterns, taking into account the effects of forest hardwood content on outbreak severity, were calculated from sequences of annual radial growth reduction for balsam fir. Thirty-one sequences, which were obtained from spruce-fir stands in a previous study at the LDTRF (see Chapter 3: Article II), were grouped into three categories according to the hardwood content of surrounding forest landscapes. Average annual and maximum annual growth reductions (%) were calculated among sequences for each landscape category (Fig. 6.2). Annual growth losses are strongly related to cumulative defoliation in a given year, which integrates a

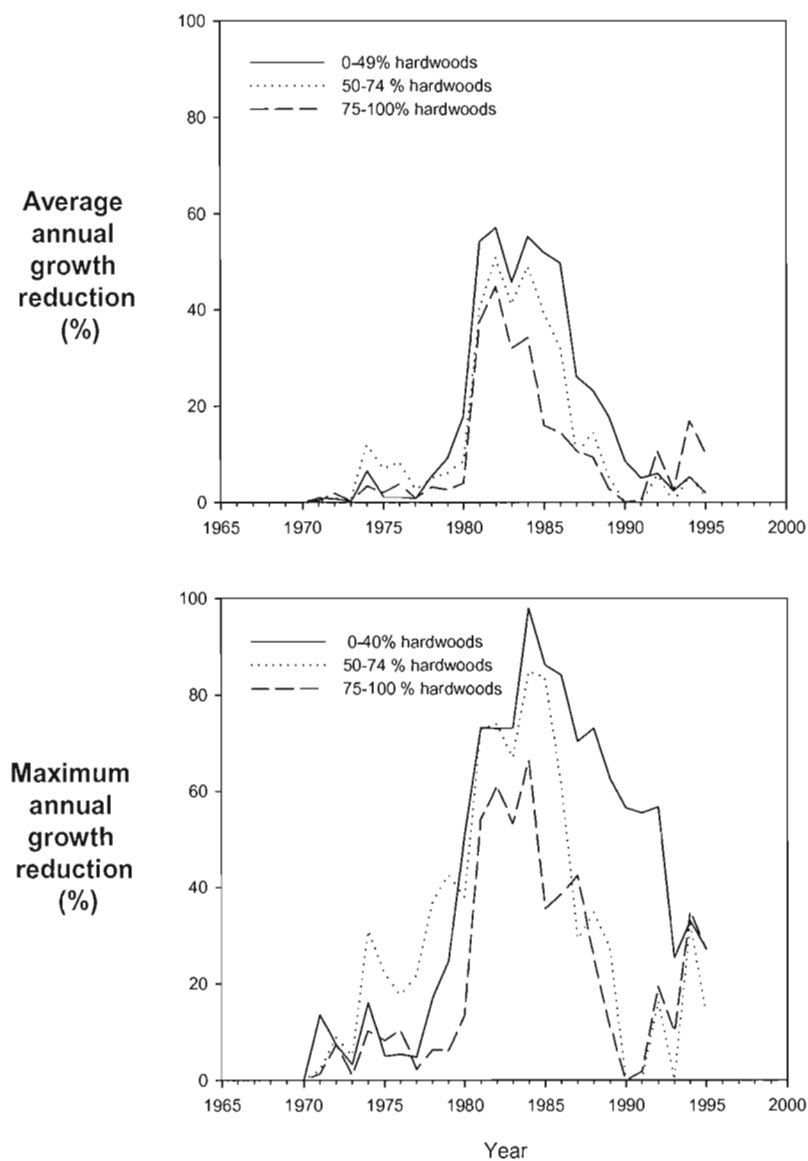


Figure 6.2. Average and maximum balsam fir growth reductions caused by the last spruce budworm outbreak in the Lac Duparquet Research and Teaching Forest. Growth data from balsam fir sampled in 31 spruce-fir stands was grouped into three categories according to the hardwood content of landscapes within 1 km of each stand: landscapes with 0-49% hardwood-dominated stands, landscapes with 50-74% hardwood-dominated stands, and landscapes where hardwood stands covered $\geq 75\%$ of surrounding landscapes.

sequence of annual foliage losses (Ostaff and MacLean 1995; Erdle and Maclean 1999). Given this, each of the average and maximum annual growth reduction sequences (Fig. 6.2), were converted to sequences of average and maximum cumulative defoliation (%), respectively, using the following polynomial equation:

$$y_t = 0.0034x_t^2 + 0.6817x_t + 10.2050 \quad (1),$$

where y_t = cumulative defoliation for year t and, x = % balsam growth reduction in year t . Derived from permanent plot measurements of balsam fir (Ostaff and MacLean 1995; Erdle and MacLean 1999), this equation describes a nearly perfect correlation ($R^2 = 0.9998$) between balsam fir growth reductions and cumulative defoliation.

Annual defoliation patterns were then estimated from the six sequences of cumulative annual defoliation. To do this, we first derived an equation to describe the relationship between these two variables using an independent set of annual defoliation sequences for New Brunswick. For each year, cumulative defoliation was calculated as a function of annual defoliation over the past 6 years using the following relationship (MacLean *et al.* 2001):

$$CD_t = (0.28C_t + 0.26C_{t-1} + 0.22C_{t-2} + 0.13C_{t-3} + 0.08C_{t-4} + 0.03C_{t-5}) \quad (2)$$

where t is year, CD is cumulative defoliation (%) and C is current defoliation (%). The coefficients for each term in the equation represent the proportion of total foliage mass retained on healthy balsam fir crowns as trees age (many needles fall as foliage ages and thus older foliage has progressively less influence on cumulative defoliation. Regression of cumulative defoliation (x) on annual defoliation (y) was calculated to derive equations describing annual defoliation as a linear function of cumulative defoliation ($R^2 = 0.78$). Using the annual cumulative defoliation sequences derived from growth reduction data as input into

the regression equation, average and maximum annual defoliation patterns for spruce/fir-dominated stands (containing < 50% hardwoods) were calculated for each of the three landscape types described above. As susceptible stands with >50% hardwood content were common in the study area, we generated another set of defoliation patterns for these stands by scaling annual defoliation for spruce/fir-dominated stands down by 43% (after the first 10 years of defoliation), the average difference between annual defoliation in stands with <50% hardwoods and >50% hardwoods (Su *et al.* 1996). Overall 12 defoliation patterns were derived from growth reduction data collected in the vicinity of the LDTRF. Patterns derived from average and maximum growth reductions represented “normal” and “severe” budworm outbreaks, respectively.

6.4.3 Implementing the SBW DSS for the LDTRF

The SBW DSS was used to simulate the impacts (volume losses) of a spruce budworm outbreak starting during 2001 in the LDTRF. A substantial effort is required to accumulate data and construct the files and databases necessary to implement the SBW DSS. Here, we briefly describe the main steps taken (Fig. 6.3), emphasizing how we deviated from the process described in detail by MacLean *et al.* (2001):

i. Compile defoliation data and calculate cumulative defoliation – typically implementation of the SBW DSS requires historical defoliation data over the last 5 years to initialize the forest condition and to determine where stands are (temporally) in forecasted defoliation patterns. As the primary objective of this SBW DSS implementation was to simulate how budworm outbreak impacts vary regionally and with forest hardwood content, we simply started an outbreak scenarios in 2001 (to date, larval counts indicate that budworm is still not at epidemic levels in the LDTRF). GIS overlays were used to assign particular forecasted defoliation patterns to stands based on stand and surrounding landscape hardwood content, when required by that scenario. For each stand, these forecasts

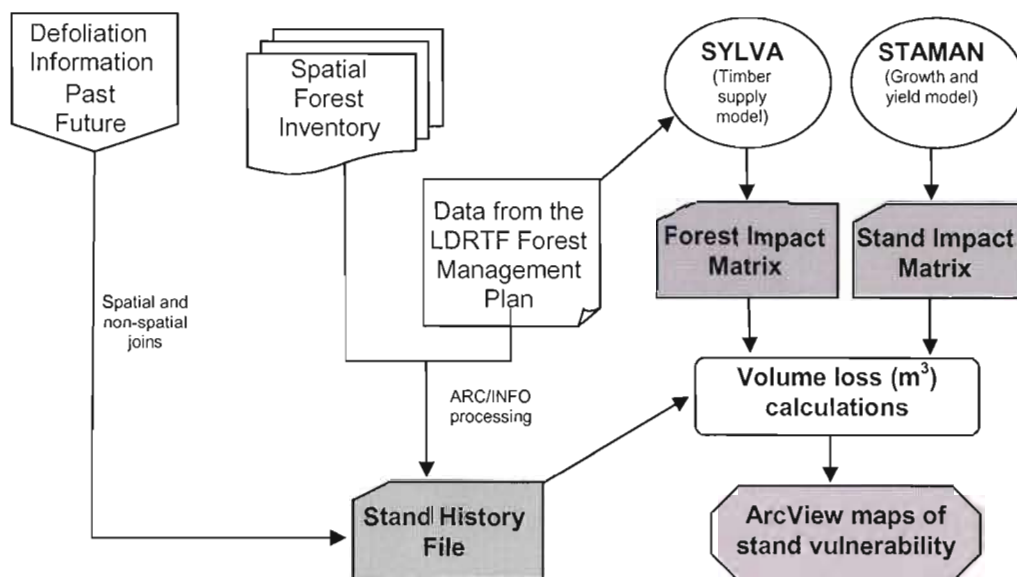


Figure 6.3. A flow-chart depicting the databases used in the SBW DSS and the processes required to calculate volume losses (m^3/ha) resulting from a future budworm outbreak on the LDTRF (modified from MacLean *et al.* 2000).

of current annual defoliation were converted to average cumulative defoliation for two successive 5-year periods using equation (2) above and dividing by 5 (MacLean *et al.* 2001). This information was recorded for each stand in the stand history file (see below).

ii. Calculate direct impacts of defoliation from the stand impact matrix –

Forest classes in the LDTRF forest management plan were matched with the 54 budworm impact classes (essentially stand types) defined by MacLean *et al.* (2001). These are delineated based on species composition and silvicultural treatment (Table 6.1) and stand age classes (not included in Table 6.1) of immature (0-40 years), mature (41-80 years), and overmature (>80 years, or >100 years for spruce-dominated stands) for natural stands, and immature (0-20 years) and mature (>20 years) for silviculturally treated stands. Once each forest type in the management plan was matched with an appropriate budworm impact class (in the LDTRF, there were a total of 41 budworm impact classes), cumulative defoliation values associated with each stand was calculated.

Because it contains relative budworm-caused losses (i.e., percentages rather than absolute volume m³/ha), the stand impact matrix (SIMPACT) developed by MacLean *et al.* (2001) is transferable from one landbase to another. Based on the representative data from permanent sample plots that were input into STAMAN (Version 2.4, Vanguard Forest Management Services Ltd. 1993; Erdle and MacLean 1999), the percent volume losses in the SIMPACT have been calculated for each of 54 budworm impact classes for all combinations of 10% cumulative defoliation classes in outbreak years 1-5 and 6-10 (MacLean *et al.* 2001). To assess direct impacts of budworm outbreaks in the LDTRF for a 5-year period, the SIMPACT, an ARC/INFO lookup table, was used to determine budworm-caused volume reduction (%) for each stand as a function of cumulative defoliation and budworm impact class.

iii. Control for indirect impacts within the forest impact matrix – In the SBW DSS, the forest impact matrix quantifies the indirect (harvest scheduling)

effects of a budworm outbreak. Budworm-caused volume losses are expected to increase the rate at which stands move through the harvest queue. The forest impact matrix is an ARC/INFO table containing ratios that reflect the change in operable growing stock in the forest (at a fixed time) for a given volume shortfall or surplus of stands scheduled for harvest (MacLean *et al.* 2001). Although the forest impact matrix is part of the regular operational SBW DSS implementation process, we did not include the effect of indirect impacts in our implementation of the SBW DSS for the LDTRF for the following reasons: i) in small forest management areas such as this one, managers are unlikely to want to endure any budworm-caused volume losses and the economic savings of not spraying infested forests with insecticide are much less than that for very large management areas and ii) the main objective of this implementation was to show, through comparison, how incorporating more regionally appropriate defoliation patterns, and defoliation patterns that varied with stand and surrounding landscape hardwood content, affect the results (i.e., total volume losses to budworm outbreaks). Normally, a 5-year harvest period over the next 35 years (i.e., a harvest period 1-7) is assigned to each stand based on management plan harvest schedule information. For the above reasons, however, we set the harvest period for all stands to 3 for our simulations. This had the effect of ensuring that all stands proceeded unharvested for the first 10 years of the outbreak cycle, by which time most stands had suffered the brunt of the budworm outbreak. Thus, SBW DSS implementation for the 11 outbreak scenarios resulted in calculation of the total volume losses for each scenario, if stands remained unsprayed to harvest period 3.

iv. Build the stand history file – for each stand on the test landbase, the stand history file contained a unique identifier, a budworm impact class number, the assigned harvest period (set at 3 for all stands), stand area (ha), 15 years of future defoliation (i.e., the forecast defoliation pattern), and the volume losses (%) calculated based on the future defoliation patterns. The volume losses in this file

were used to generate maps of budworm impact for the outbreak scenarios implemented on the LDTRF. These maps can be used to prioritize future forest areas for protection strategies to reduce budworm losses (e.g., insecticide spraying, pre-emptive harvesting). The stand history file was also used to tabulate the area of forest covered by the following budworm impact classes: 1-10, 11-20, 21-40, 41-60, and 61-80% volume losses. Using this tabulated information, we were able to compare the outcome of 11 outbreak scenarios implemented for the LDTRF.

6.5 Results and Discussion

6.5.1 Comparison of Annual Defoliation Forecasts

In parts of eastern Canada, management to reduce the impacts of budworm outbreaks has aimed at keeping annual defoliation levels below 40%, which results in some growth reduction but limited host tree death (Erdle and MacLean 1999; MacLean *et al.* 2001). The SBW DSS calculates volume losses as the difference between the volume yield that incorporates the impact of a budworm outbreak when annual defoliation is 40% (i.e., minimum acceptable losses) and the volume yield where defoliation is unrestricted (MacLean *et al.* 2001). Thus, the seventeen defoliation forecasts derived from historical data were compared within the context of this reference point (Fig. 6.4).

While all defoliation patterns representing normal outbreaks (forest hardwood effects excluded; Fig. 6.4a, d, f) had 6 to 7 years of defoliation >40%, maximum annual defoliation for the New Brunswick pattern was about ~20% higher than the normal patterns derived from Quebec aerial survey data and host growth reduction data (Fig. 6.4d, f). Defoliation patterns representing severe budworm outbreaks (forest hardwood effects excluded; Fig. 6.4b, c, e) had 9-12 years of defoliation >40%. Among these years, however, annual defoliation for the Gray *et al.* (2000) pattern (Fig. 6.4c) was on average, ~20% lower than defoliation for the other two patterns. The methods these

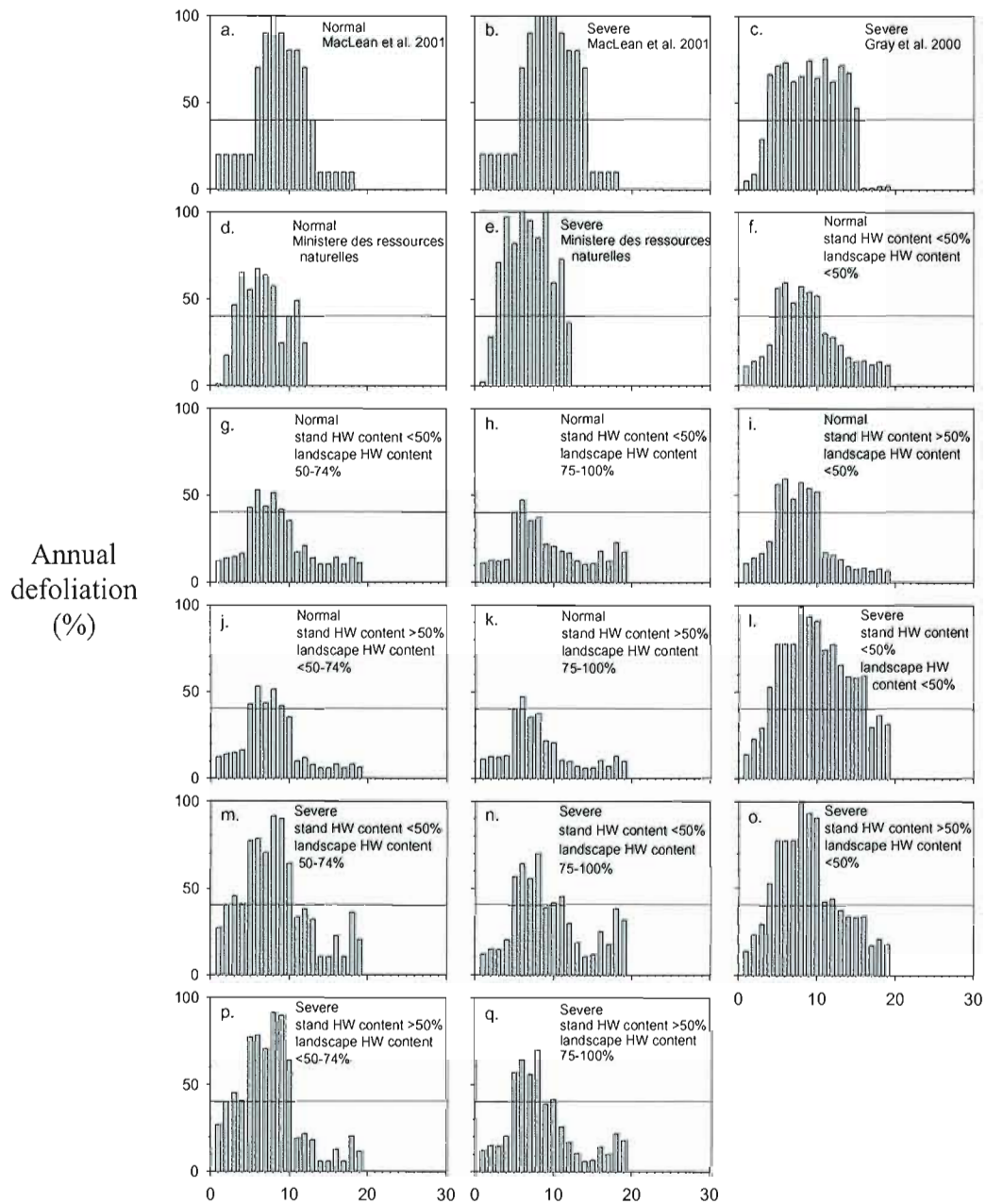


Figure 6.4. Historical defoliation patterns used to project the potential timber volume losses caused by a future budworm outbreak in the Lac Duparquet Research and Teaching Forest of northwestern Quebec. Historical defoliation patterns were obtained from the literature (a-c), summarized from aerial sketch map data of budworm-caused defoliation in the region (d-k), and derived from growth reduction data collected near the test landbase and grouped by the hardwood content of stands (< 50% or $\geq 50\%$) and the proportion of hardwood-dominated forests in landscapes (< 50%, 50-74%, 75-100%). Patterns representing “normal” or “severe” budworm outbreaks are indicated on the graphs, as are the citations for defoliation patterns obtained from the literature.

authors used to calculate annual defoliation from aerial sketch map data meant that annual defoliation could never be greater than 80%, and this probably underestimates defoliation levels for severe outbreaks.

The twelve patterns derived from growth reduction data collected at the LDTRF (Fig. 6.4f -q) permit an evaluation of forest hardwood effects on defoliation levels. Among “normal” defoliation patterns, the number of years with >40% defoliation decreased from 6 to 5 to 2 years as surrounding landscape hardwood content increased from <50% to 50-74% to 75-100%, respectively, for all stand hardwood contents (Fig. 6.4f-k). Differences in defoliation patterns among stands with <50% and >50% hardwoods reflect the 43% downward scaling of defoliation after the first ten years of the outbreak; ten years after the start of a “normal” outbreak, however, annual defoliation was <40% for all years of all patterns (Fig. 6.4f-k). Among “severe” outbreaks in spruce-fir dominated stands, the number of years with >40% defoliation decreased from 13 to 8 to 6 years as surrounding landscape hardwood content increased from <50% to 50-74% to 75-100%, respectively (Fig. 6.4l-n). Among severe outbreak in mixedwood stands (>50% hardwood content; Fig. 6.4o-q), the number of years with >40% defoliation decreased from 13 to 8 to 6 years as surrounding landscape hardwood content increased from <50% to 50-74% to 75-100%, respectively.

6.5.2 Projected Volume Losses for the LDTRF

Of the 11 outbreak scenarios applied to the LDTRF (Table 6.2), the first seven were used to evaluate the implications of using defoliation patterns from different regions (and data sources) to project volume losses (m^3/ha) (Table 6.2). Total budworm-caused losses projected using defoliation patterns indicative of a normal outbreak in Quebec were about 19 000 and 21 000 m^3 (scenarios 3 and 4; Table 6.2), about 20% of the losses projected using the defoliation pattern for New Brunswick (scenario 1; Table 6.2). Mean and maximum stand losses ranged from 3 - 41 m^3/ha under the normal outbreak scenarios (Table 6.2). While projections using the Quebec defoliation patterns indicated that the impact of an outbreak would be low over ~ 5 700 ha of the LDTRF, projections

Table 6.2. Potential budworm-caused volume losses in for 11 budworm outbreak scenarios simulated for the Lac Duparquet Research and Teaching Forest (LDTRF) in northwestern Québec.

Scenario	Defoliation pattern(s) used ^a	Stand budworm losses (m ³ /ha)		Area (ha) of LDTRF covered by budworm volume loss class				Total budworm-caused losses (m ³) ^b
		mean	max.	Low (1-20 m ³ /ha)	Moderate (21-40 m ³ /ha)	High (41-60 m3/ha)	Extreme (>61 m ³ /ha)	
Budworm outbreak scenarios using defoliation patterns for New Brunswick:								
1	a Normal outbreak	15	41	4 052	1 752	28	0	91 626
2	b Severe outbreak	25	71	2 693	2 296	739	105	148 164
Budworm outbreak scenarios using defoliation patterns for northwestern Quebec:								
Normal outbreak								
3	d (aerial survey data)	4	9	5 781	0	0	0	21 399
4	f (growth data)	3	9	5 708	0	0	0	18 698
Severe outbreak								
5	c (Gray <i>et al.</i> 2000)	11	30	5 041	791	0	0	64 303
6	e (aerial survey data)	29	84	2 376	2 036	1 238	181	171 721
7	l (growth data)	25	70	2 487	2 380	874	91	148 027

Table 6.2 (cont)

Budworm outbreak scenarios using Quebec defoliation patterns that incorporate forest hardwood content effects:Normal outbreak

8	f, g, h landscape hardwood effect included	2	9	4 225	0	0	0	13 699
9	f, g, h, i, j, k stand and landscape hardwood effect included	2	9	4 194	0	0	0	13 617

Severe outbreak

10	l, m, n landscape hardwood effect included	21	70	3 231	1 879	734	88	126 430
11	l, m, n, o, p, q stand and landscape hardwood effect included	19	70	3 524	1 482	706	88	114 479

^a For each of the 11 outbreak scenarios run for the LDTRF, the lower case letters refer to defoliation pattern(s) used and these appear in Figure 6.3.

^b total budworm-caused losses equal the total volumes lost (m³) over the entire landbase.

using the New Brunswick pattern indicated that the impact of an outbreak would be moderate and high on 1 752 ha and 28 ha of the landbase, respectively (Table 6.2).

Potential total volume losses projected under severe outbreak (scenarios 2, 5-7; forest composition effects excluded) were greatest using the scenario derived from aerial survey data in Quebec (i.e., scenario 6; $\sim 171\,000\text{ m}^3$; Table 6.2). Total losses projected under scenario 2 and 7 were 14% lower than projected under scenario 6 and 63% lower than the scenario 5, which uses the northwest Quebec defoliation pattern obtained from Gray *et al.* (2000). Under a severe outbreak, mean stand losses ranged from 11 to 29 m^3/ha and maximum stand losses ranged from 30 to 84 m^3/ha . Except for scenario 5, all severe outbreak scenarios generated low, moderate, high and extreme budworm impact on the test landscape (Table 6.2); in all cases, most of the landbase was of the low volume loss class (i.e., 1-20 m^3/ha).

Differences in the projected losses among normal outbreak scenarios 1, 3, and 4 and among severe outbreaks scenarios 1, 5, 6, and 7 could be explained in number of ways. It is possible that the differences among the normal scenarios are a result of differences in the regional dynamics of budworm populations. Royama *et al.* (2005) showed that while budworm populations increase and decrease in unison, the amplitude of these increases, and thus the severity of annual defoliation during outbreaks, can vary from region to region. Gray *et al.* (2000) report substantial spatial variation in defoliation patterns across Quebec during the last budworm outbreak, with a tendency for more severe outbreaks to occur near the Quebec-New Brunswick border. Candau and Fleming (2005) studied spatial patterns in defoliation over Ontario and found that defoliation was less frequent (from 1967 and 1998) in northern than southern Ontario. This variation in defoliation patterns along a latitudinal gradient in Ontario was significantly related to a northward decrease in winter temperatures. As winters in the boreal forests of Quebec are colder than those in New Brunswick (Environment Canada 2002), it is possible that limited budworm larval survival associated with cold winter temperatures (Régnière 1982; Harvey 1985) accounts for the lower volume losses projected using defoliation patterns from Quebec than those using the defoliation

patterns from New Brunswick. However, projected volume losses under severe outbreak scenarios using defoliation patterns for Quebec were about the same, and even greater, than those using the defoliation pattern derived for New Brunswick (Table 6.2, scenarios 6 and 7 vs. scenario 2) suggest that climatically driven differences in defoliation patterns may not be enough to account for differences in our projected volume losses.

The type of data from which forecasted defoliation patterns were derived, and the way the forecasts were derived, probably also contributes to the greater variation than expected among losses projected for normal and severe outbreaks (i.e., scenarios 1, 3, 4 and scenarios 2, 5-7, respectively; Table 6.2). For example, while the defoliation patterns for New Brunswick come from host-dominated forests where outbreaks have the largest impacts (MacLean 1980; see Chapter 3 - Article II), the patterns derived from aerial survey and growth data in Quebec have been averaged over a gradient of forest hardwood content. Because of this, application of the New Brunswick pattern to all susceptible stands on a landbase, particularly when mixedwoods are common, will likely overestimate volume losses. The severe defoliation pattern described by Gray *et al.* (2000) for Quebec suffers another pitfall in that it will inevitably underestimate the impacts of severe outbreaks over a landscape because mean annual defoliation was calculated using the midpoints of defoliation categories, such that the maximum annual defoliation level could never exceed 80%. During the peak of an outbreak, however, spruce budworm typically removes all current year foliage (Baskerville and MacLean 1979; Ostaff and MacLean 1995).

Under both normal and severe outbreak scenarios, projected volume losses were substantially lower when the effects of forest hardwood content were incorporated into model simulations. Simulations of a normal outbreak that took into account the effects of stand and surrounding landscape hardwood on annual defoliation (i.e., scenarios 8 and 9; Table 6.2) projected volume losses 27% less than the projected loss of ~18 000 m³ for the scenario that did not consider forest hardwood content effects on defoliation (i.e., scenario 4; Table 6.2). Mean and maximum stand volume losses were 2 and 9 m³/ha,

respectively. Projections incorporating forest hardwood effects indicated budworm could have a low impact (i.e., 1-20 m³/ha) over the entire area affected (i.e., ~ 4 200 ha) under a normal outbreak (Table 6.2). Severe outbreak simulations that took into account the effects of stand and surrounding landscape hardwood on annual defoliation (i.e., scenarios 10 and 11; Table 6.2) projected volume losses 22.5% and 14.5 % less than the projected loss of ~148 000 m³ for the scenario that did not consider forest hardwood content effects on defoliation (i.e., scenario 7; Table 6.2). Under severe outbreaks, mean and maximum potential volume losses were ~ 20 to 70 m³/ha and the area covered by the outbreak would include all impact classes: low, moderate, high, and extreme (Table 6.2). Projected losses were not substantially different between the normal outbreak scenario including landscape effects alone (scenario 9) and stand and landscape effects together (scenario 10), because annual defoliation most years was < 40%, the defoliation threshold delineating minimal acceptable losses. Our results indicate that model projections not taking into account the effect of forest hardwood content will likely overestimate budworm-caused volume losses. A number of studies have recently shown that stands mixed with hardwoods contain more abundant parasitoids and other natural budworm enemies that help keep budworm populations low (Cappuccino *et al.* 1998; Quayle *et al.* 2003).

Substantial volume reductions caused by budworm outbreaks may make a stand economically unviable to harvest. Most forest management plans specify an operability limit of 50 m³/ha. Figure 6.5 shows the potential effects of a severe outbreak scenario on volume yield for 6 of the 14 susceptible stand types in the LDTRF. Volume yields for balsam fir and white spruce stands (BFSP) dropped below the operability limit 11 to 16 years after the start of the outbreak if surrounding forest landscapes contained <50% hardwood stands. Projected yields for BFSP stands were about 20% greater if the stand was sprayed with insecticide and if surrounding forest landscapes had >50% hardwood-dominated forests. Projected volume yields did not decrease below the operability limit for any of the other five stands (Fig. 6.5). Except for the SPBF stand type, which was

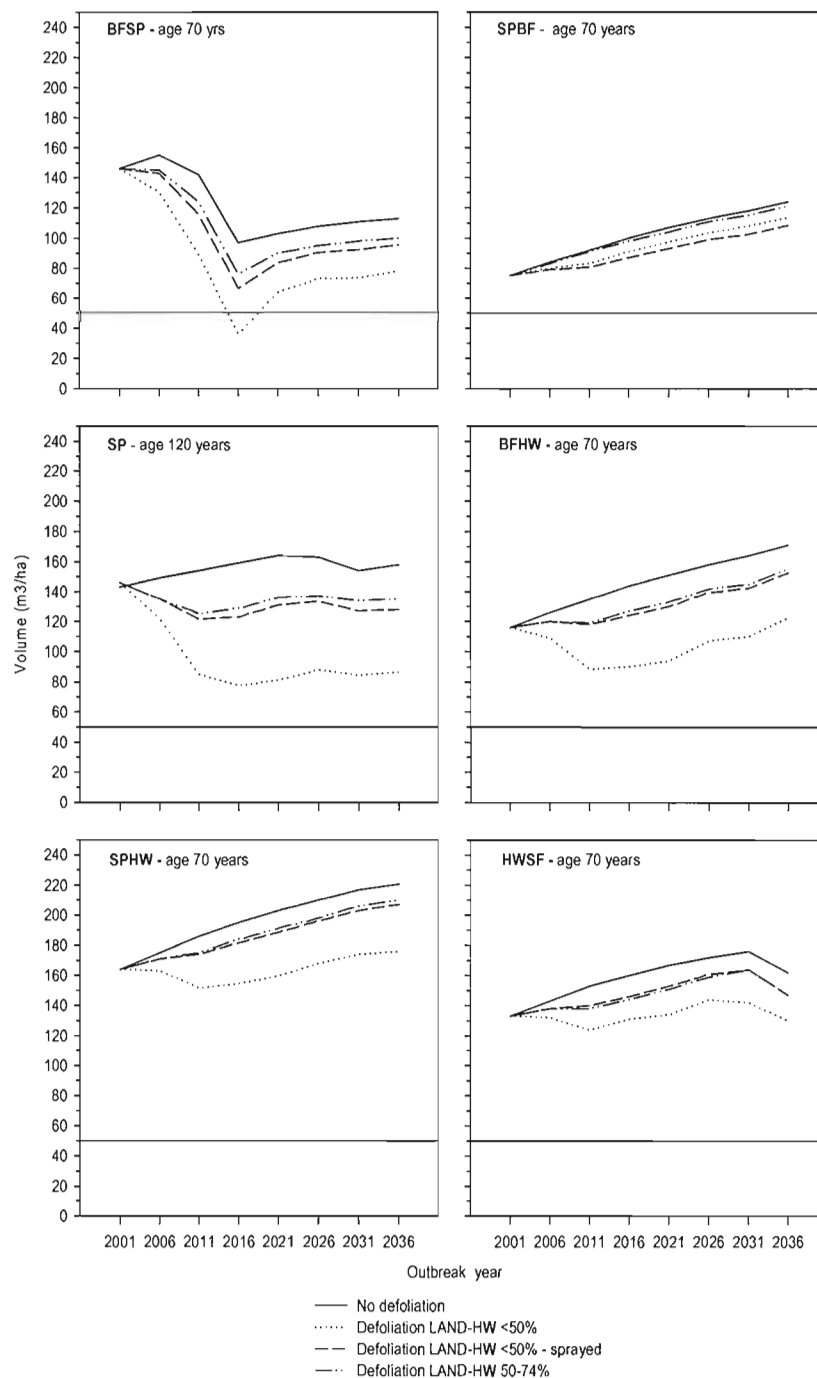


Figure 6.5. Effects of landscape hardwood content on volumes losses during a severe budworm outbreak in spruce-fir dominated stands (a-c) and mixedwoods (d-f). Simulations were undertaken using an outbreak start year of 2001. Table 6.2 indicates stand codes and abundance of these stands in the LDTRF. LAND-HW = landscape hardwood content (%).

largely unaffected by the outbreak, insecticide spraying and greater landscape hardwood content had the same effect for other stand types: greater stand yields. Among the five stands affected by the outbreak, hardwood stands mixed with spruce and fir (HWSF), which cover most of the LDTRF, had the least volume losses.

Figure 6.6 shows a potential volume loss map for the LDTRF under a severe outbreak scenario, when defoliation patterns from data collected in Quebec are applied to the landscape, and forest hardwood content is taken into account. The map identifies the stands of low, moderate, and high vulnerability to future spruce budworm outbreaks. The most vulnerable stands, indicated in red, are likely to lose $>41 \text{ m}^3$ wood.

6.6 Conclusions

Although Gray *et al.* (2000) report that the large-scale spatio-temporal pattern of the current budworm outbreak is unfolding in a manner similar to the last budworm outbreak in Quebec, it has been argued that historical budworm outbreak and defoliation patterns are unlikely to be repeated, making projections of future outbreak impacts unreliable (Royama *et al.* 2005). We agree that defoliation patterns in stands are likely to vary in time — as might the summation of resulting volume losses over a managed landscape — given variations in forest composition (see Chapter 2: Article I and Chapter 3: Article II) and expected changes in regional climate (Flannigan *et al.* 2000). However, incorporating any number of plausible defoliation forecasts into an implementation of the SBW DSS can take this into account.

Seventeen defoliation forecasts derived from historical data were applied singly, and in combination to stands, in order to project volume losses under 11 outbreak scenarios for the LDTRF. There was considerable variation in volume losses projected for these scenarios. Some of this variation can be attributed to characteristics of data sources and the way in which defoliation forecasts were derived. Because of this, it was difficult to

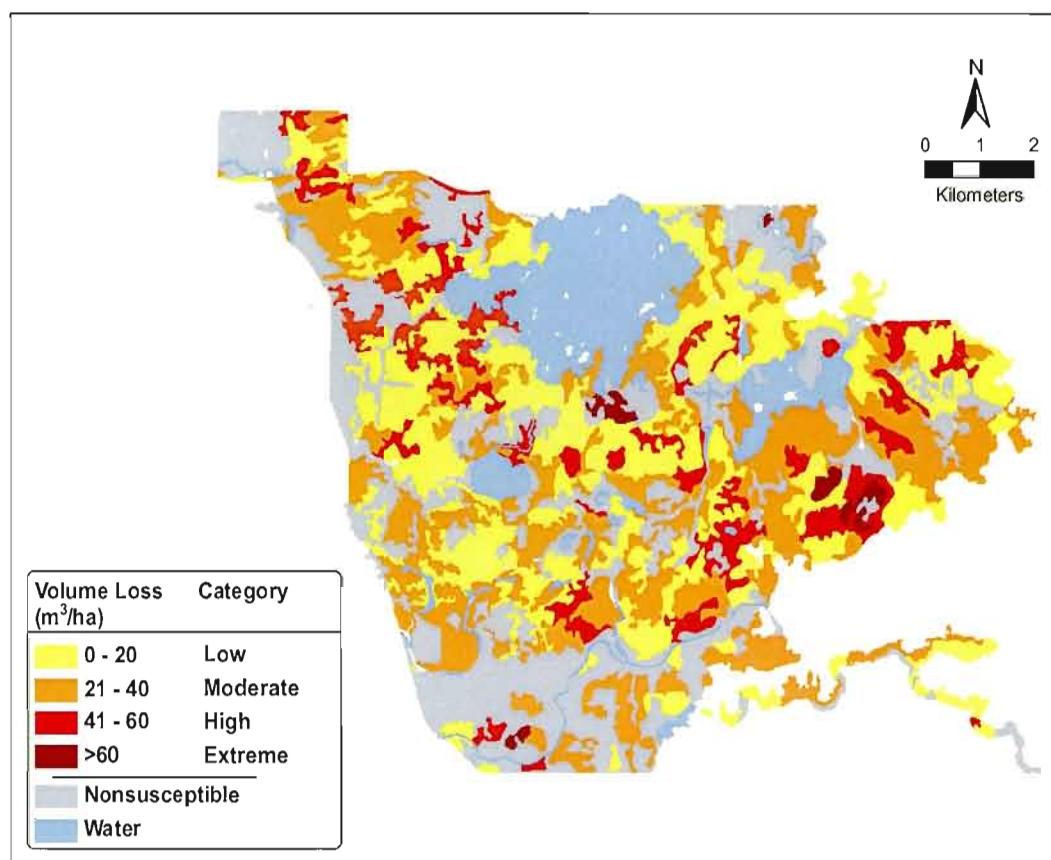


Figure 6.6. Example of a map showing volume losses caused by a severe budworm outbreak at the Lac Duparquet Research test landbase in northwestern Quebec. This map represents the worst case scenario, for projections including the effects of forest hardwood content on outbreak severity (i.e., scenario #11; Table 6.2).

definitively determine if using defoliation patterns from a different region (i.e., New Brunswick) accounted for the variations in projected volumes losses for the LDTRF. Given recent research indicating regional variation in budworm population dynamics and defoliation (Gray *et al.* 2000; Royama *et al.* 2005; Candau and Fleming 2005), we expect that this should occur, and recommend the SBW DSS use defoliation patterns specific to the region in which it is implemented. While the implications of using defoliation patterns from different regions was difficult to assess, our results clearly demonstrate that volume losses projected by the SBW DSS may be over-estimated by 23 to 27%, if the effects of forest hardwood content on annual defoliation levels are not taken into account. To date, implementations of the SBW DSS have applied a single defoliation pattern to all stands in a managed landscape. To obtain the “best” estimate of future volume losses, we recommend that future SBW DSS implementations apply multiple defoliation patterns to a landscape so that the impacts of an outbreak in each stand are reflective of stand and surrounding forest hardwood content.

Eighty-one percent of the LDTRF is susceptible to a future spruce budworm outbreak. Simulation of a severe outbreak that takes into account forest composition effects projected that up to 114 749 m³ of balsam fir and spruce could be lost during a future spruce budworm outbreak in the LDTRF. Model projections showing a range of losses associated with a worst case scenario (i.e., severe outbreak), and identification of the most susceptible stands on the landscape, can help to guide forest management to reduce the impacts of a future budworm outbreak on wood supplies, and on other forest values (e.g., old-growth retention targets, wildlife habitat, biodiversity, etc.) in the LDTRF.

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7 CONCLUSIONS

Il y a une préoccupation croissante que les activités anthropiques ainsi que les changements climatiques modifient sensiblement les régimes de perturbations naturelles des forêts en plus d'augmenter les risques de perturbations catastrophiques, de changements environnementaux indésirables et de pertes de biens et services rendus par les écosystèmes, ce qui aura des impacts socio-économiques sans précédent (Dale *et al.* 2001; Drever *et al.* 2006). Notre capacité à prévoir ces risques et à se préparer au futur dépend d'une connaissance fondamentale des régimes de perturbations naturelles des forêts. Les études sur la variabilité historique des régimes de perturbations naturelles pourront contribuer à cette tâche (Swetnam *et al.* 1999). Cette thèse a décrit les patrons historiques des épidémies de la tordeuse des bourgeons de l'épinette (TBE) en relation avec la composition de la forêt, les activités historiques de gestion forestière, et la variabilité du climat dans l'est du Canada. Quoique des études aient décrit la sévérité des épidémies en relation avec de la composition des peuplements (MacLean 1980; Bergeron *et al.* 1995 ; Su *et al.* 1996), l'influence de la composition de la mosaïque forestière sur la sévérité des épidémies dans les peuplements dominés par des espèces hôtes a été peu étudiée, avec des résultats contradictoires (Bergeron *et al.* 1995; MacKinnon *et al.* 2003). Aussi, aucune étude jusqu'à celle-ci, n'a porté sur l'influence de la composition de la mosaïque forestière à de multiples échelles. En plus, les études décrivant les relations entre la sévérité des épidémies et les patrons spatiaux et temporels du climat étaient très limitées.

Utilisant une approche dendrochronologique, j'ai reconstitué la dynamique temporelle des épidémies de TBE dans des peuplements de la forêt boréale québécoise n'ayant pas été perturbés par les feux depuis 1760. Les patrons de réductions de croissance radiale ont indiqué que les épidémies de TBE se sont produites à tous les 30-36 ans, celles de la fin du 20^{ième} siècle ayant été les plus longues. Au contraire de ce qui est rapporté dans la littérature, j'ai trouvé que l'occurrence périodique des épidémies n'était pas liée à une augmentation des périodes de sécheresse, pas plus qu'elle ne

semblait suivre les cycles d'abondance des espèces hôtes. Comme Royama *et al.* (1984; 2005) ont suggéré, l'occurrence cyclique des épidémies est probablement davantage reliée aux cycles des ennemis naturels et, probablement, à d'autres caractéristiques intrinsèques de leur dynamique des populations (Ginzburg et Taneyhill 1994). Bien que la fréquence des épidémies ait été relativement constante, la durée et la sévérité des épidémies semblent être devenues plus variables. Une tendance vers des épidémies plus longues et plus sévères correspond au cycle d'abondance du sapin baumier mature. Ceci, et l'augmentation de température depuis 1850, peut probablement expliquer les plus longues épidémies (et la présence des deux vagues distinctes d'épidémies) à la fin de la 20^{ième} siècle.

Parce que la structure et la composition des forêts changent rapidement en réponse aux activités anthropiques et les changements climatiques, il devient de plus en plus important de comprendre comment les processus écologiques à l'échelle du peuplement forestier sont liés aux processus écologiques à l'échelle des paysages environnants. J'ai examiné l'influence de la composition de la mosaïque forestière et des caractéristiques des peuplements sur la sévérité de la dernière épidémie de TBE dans des peuplements dominés par le sapin baumier et l'épinette de la région boréale du nord-ouest du Québec (1970-1986). J'ai trouvé que la variabilité de la suppression de croissance radiale causée par la TBE est surtout reliée à l'abondance des hôtes dans les peuplements et au pourcentage des paysages environnant occupé par des peuplements feuillus. Les épidémies les plus sévères se sont produites dans des peuplements où les hôtes matures étaient abondants et où la proportion du paysage environnant dominée par les feuillus était faible. Bien que l'amplitude du gradient d'abondance des hôtes dans les peuplements soit moins grande que l'amplitude du gradient de dominance en peuplements feuillus à l'échelle du paysage environnant, la première variable a expliqué 8% de plus de la variation de la sévérité des épidémies. Par conséquent, et même si mes résultats soutiennent l'hypothèse selon laquelle la composition du paysage environnant affecte la sévérité des épidémies, les effets locaux sont probablement les plus forts. Le fait que les épidémies soient moins sévères dans les paysages dominés par les

peuplements feuillus s'inscrit dans la lignée des résultats obtenus dans cette même région par Bergeron *et al.* (1995) et s'expliquent probablement par de plus grandes abondance et diversité en ennemis naturels de la tordeuse (Cappuccino *et al.* 1998; Quayle *et al.* 2005). Cependant, et comme ce fut le cas dans d'autres études du même genre (e.g., Thies *et al.* 2003), les variables décrivant la composition des paysages forestiers sont fortement corrélées entre elles. Il est donc difficile d'éliminer la possibilité que certaines de ces variables (e.g., l'abondance des peuplements dominés par le sapin) influencent d'autre processus reliés à la dynamique des populations de la tordeuse (e.g., dispersion, fécondité), affectant ainsi la sévérité dans les peuplements hôtes. Aussi, les insectes peuvent réagir en fonction de la composition du paysage à de multiples échelles. L'influence de l'abondance des peuplements feuillus dans les paysages environnant sur la sévérité des épidémies a été testée à deux échelles spatiales (500 m et 1000 m). Il s'est avéré que l'abondance de forêts feuillues à l'intérieur d'un voisinage de 1000 m des peuplements visés a la plus grande influence. Les autres études ayant porté sur l'influence de la composition de la mosaïque forestière environnante sur la sévérité de la défoliation par les herbivores ont détecté des effets significatifs entre 53 à 2500 m des peuplements d'hôtes. Une extension intéressante à cette étude serait d'examiner les effets de l'abondance des peuplements feuillus à l'intérieur d'une plus grande plage de voisinages (e.g., 50 m - 4000 m).

Dans un plus grand territoire situé dans le nord du Nouveau-Brunswick, j'ai examiné les influences relatives de la localisation géographique (latitude et longitude), de l'altitude, de l'abondance des feuillus dans la mosaïque forestière, et de l'historique d'épandage d'insecticides sur la sévérité de la suppression de croissance radiale causée par les épidémies de la tordeuse. La localisation géographique des peuplements échantillonnés explique la plus grande proportion de la variabilité de la sévérité des épidémies et des résultats préliminaires suggèrent que les épidémies sont plus sévères là où les hivers sont plus chauds. Une étude de Candau et Fleming (2005), portant sur les patrons de défoliation en relation avec les variations du climat en Ontario, supportent cette hypothèse. Nos résultats pour le Nouveau-Brunswick, conjugués à ceux obtenus

dans le nord-ouest du Québec, soulignent l'importance de considérer le contexte spatial des peuplements afin d'évaluer leur vulnérabilité aux épidémies de TBE. La sévérité des épidémies est faiblement reliée à l'épandage d'insecticide et à l'altitude. D'autres études ont rapporté des résultats semblables (Fleming *et al.* 1984; Hardy *et al.* 1986).

La mortalité du sapin baumier résultant des épidémies de TBE génère des trouées à l'intérieur desquelles la disponibilité de ressources telles que la lumière, l'humidité et l'espace augmentent. Les caractéristiques physiques de ces trouées (e.g., la taille), et leur taux de formation, sont fortement liés à la synchronisation et à l'étendu de la mortalité (Kneeshaw et Bergeron 1998; D'Aoust *et al.* 2004). J'ai observé que les patrons spatio-temporels de mortalité au sein des peuplements hôtes varient en relation avec l'abondance des peuplements feuillus dans la mosaïque forestière environnante, la mortalité étant étalée sur une période de temps plus courte dans les peuplements entourés de peu de peuplements feuillus. Cela implique que les trouées produites en périodes épidémiques sont plus grandes et apparaissent de façon plus rapidement, lorsque la proportion du paysage environnant occupée par des peuplements feuillus est faible avec d'importantes répercussions possibles sur les patrons de succession. Bien que plusieurs mentions de successions cycliques, où la régénération haute en sapin remplace les arbres morts, peuvent être trouvées dans la littérature (Baskerville 1975; MacLean 1988; Morin 1994; Bouchard *et al.* 2005), les résultats de cet étude suggèrent que les patrons de succession suivant les épidémies soient plus complexes. Quatre voies successioneles possibles, en relation avec la proportion de peuplements feuillus dans le paysage environnant, sont proposées.

À ce jour, implémentation du le Système d'aide a la Décision pour la Tordeuse des Bourgeon de l'Épinette SAD TBE à travers le Canada a été faite à partir des patrons de défoliation observés au Nouveau-Brunswick (*cf.* MacLean *et al.* 2001). Cependant, les résultats de cette thèse, tout comme ceux d'autres études (Su *et al.* 1996; Gray *et al.* 2000; MacKinnon et MacLean 2003), montrent la variabilité intra- et inter-régionale des patrons de défoliation est considérable. Pour améliorer les prévisions de pertes en bois (m^3) à cause d'une future épidémie, cette variabilité devrait être considérée dans les

implémentations du SAD TBE. En utilisant les données récoltées au cours de cette étude, j'ai incorporé les effets de la composition de la mosaïque forestière et de la composition des peuplements sur les patrons de défoliation aux modèles du SAD TBE pour estimer les pertes de volumes de bois entraînées par une épidémie future sur un territoire pilote situé au Québec – la Forêt d'Enseignement et de la Recherche du Lac Duparquet (FERLD). J'ai comparé les résultats de simulations se basant sur les patrons propres à cette région (Gray *et al.* 2000) avec ceux obtenus à partir des patrons de défoliation du Nouveau-Brunswick (MacLean *et al.* 2001). Les simulations suggèrent qu'omettre l'effet de la composition des forêts entraîne une surestimation des pertes d'au moins 23 %. Environ 80% de la FERLD est vulnérable à la prochaine épidémie de TBE et la simulation d'une épidémie incorporant l'effet de la composition des forêts sur la vulnérabilité des peuplements prédit des pertes de bois de $\sim 114\,000\text{ m}^3$. Cette information, conjuguée à l'utilisation de cartes indiquant les peuplements les plus vulnérables, pourrait être utilisée afin de planifier un aménagement des forêts visant à réduire les impacts d'une épidémie future sur les approvisionnements en bois et d'autres composantes importants de la forêt (e.g., vieilles forêts, habitats fauniques, biodiversité, etc.). Cependant, il est important d'évaluer la pertinence d'utiliser les patrons historiques et d'en reconnaître les limites. Il a en effet été avancé qu'il est peu probable que les patrons historiques de défoliation se reproduisent avec précision, rendant des prévisions des impacts d'épidémies futures incertaines. Toutefois, Gray *et al.* (2000) affirment que les patrons spatio-temporels des épidémies de tordeuse et de défoliation observés récemment au Québec ressemblent, à l'échelle régionale, à ceux de l'épidémie précédente. En se basant sur la relation entre l'abondance des parasitoïdes de la tordeuse et l'abondance de feuillus (Cappuccino *et al.* 1998; Quayle *et al.* 2003), il est en effet plausible que la relation entre la sévérité des épidémies et la composition des forêts, à l'échelle du paysage, restera relativement stable, au moins pour la durée de la prochaine épidémie. Il est toutefois possible que les changements climatiques en cours affectent ces interactions entre la composition de la forêt et la communauté de parasitoïdes de la tordeuse.

Plusieurs craignent qu'un déclin de la biodiversité ait des répercussions importantes sur la résilience écologique et socio-économique des écosystèmes face aux perturbations futures (Folke *et al.* 2004; Drever *et al.* 2006). Certains chercheurs avancent que les écosystèmes riches en espèces plantes sont moins vulnérable aux épidémies d'insectes (Root 1973; Cappuccino *et al.* 1998; Jactel 2005) parce que cette diversité : i) réduit la disponibilité en hôtes et ii) augmente le contrôle des populations d'insectes par les ennemis naturels. Bien que cette idée soit toujours débattue (Koricheva *et al.* 2006), les résultats de cette thèse semblent pencher en faveur de cette hypothèse. Je propose donc que d'éventuelles stratégies d'aménagement forestier ayant pour un objectif d'atténuer les impacts écologiques et socio-économiques des épidémies de TBE impliquent des efforts pour maintenir une proportion significative de peuplements feuillus dans les paysages.

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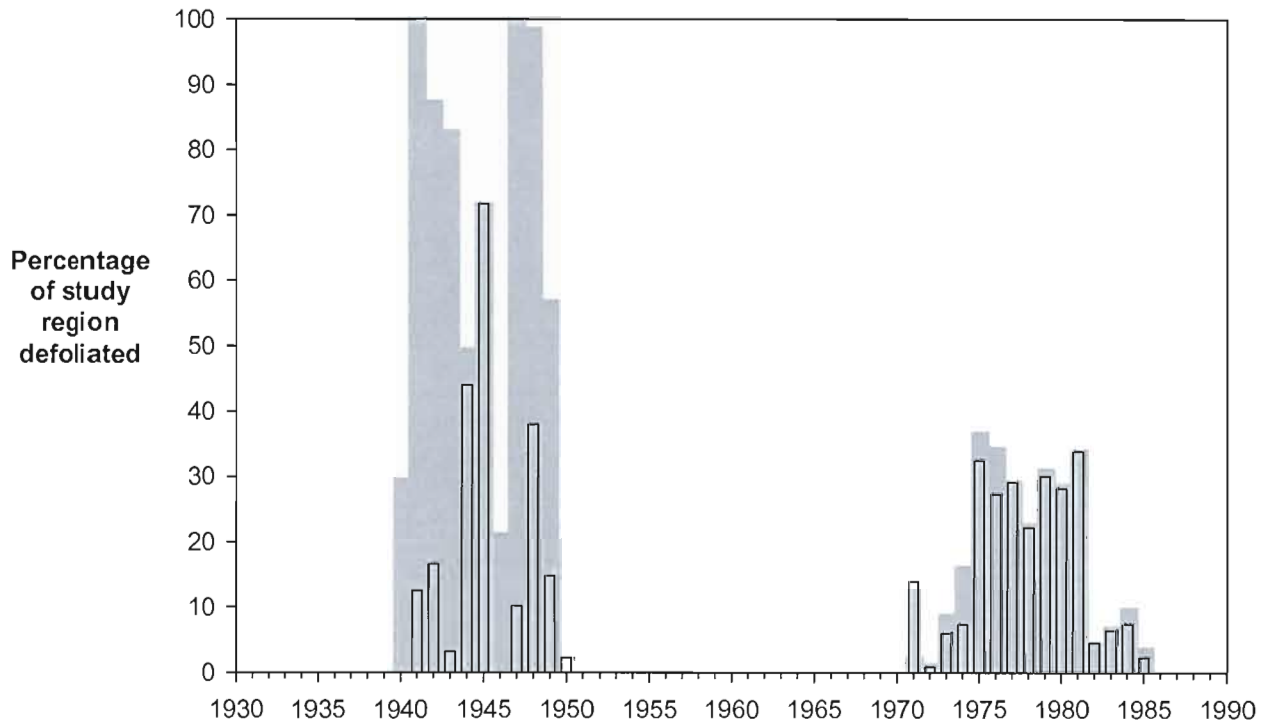
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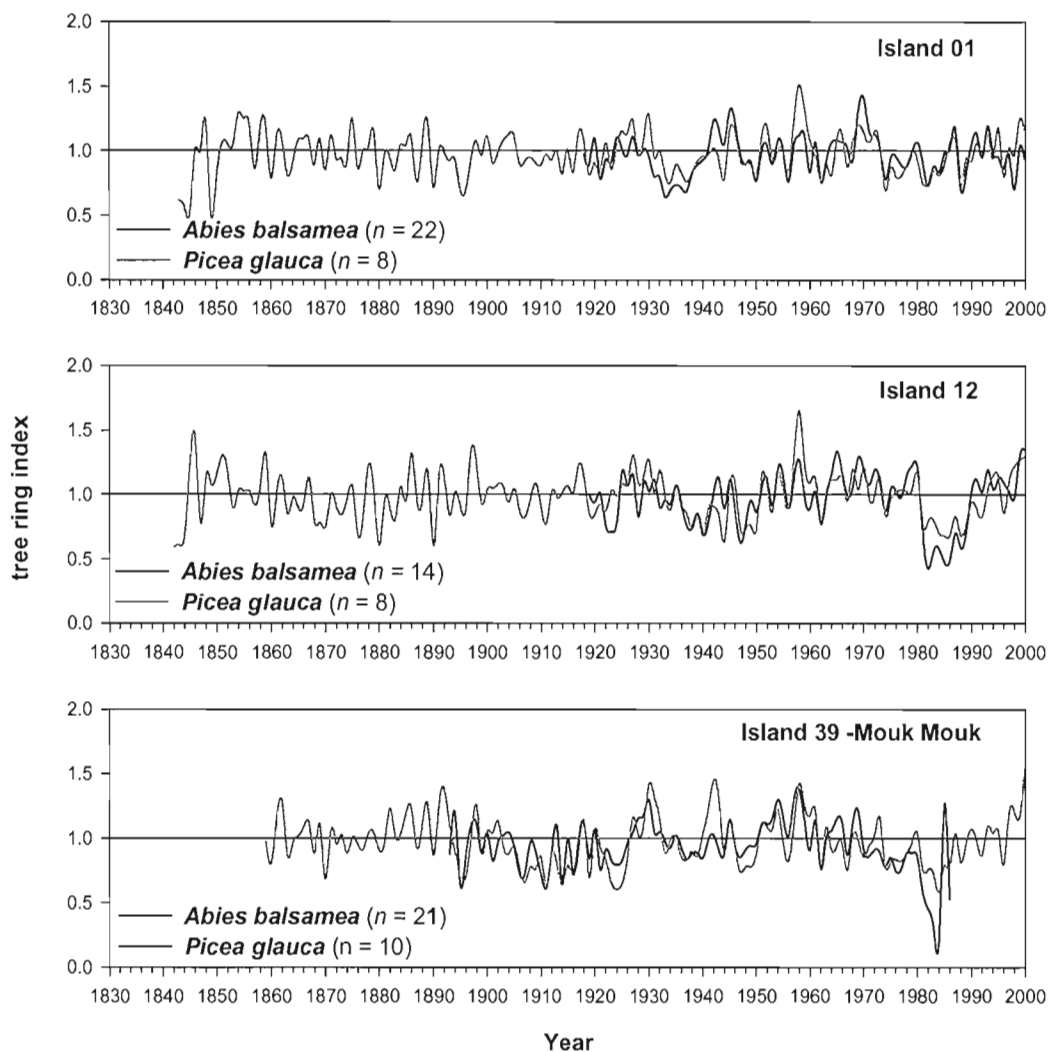
9 ANNEXES

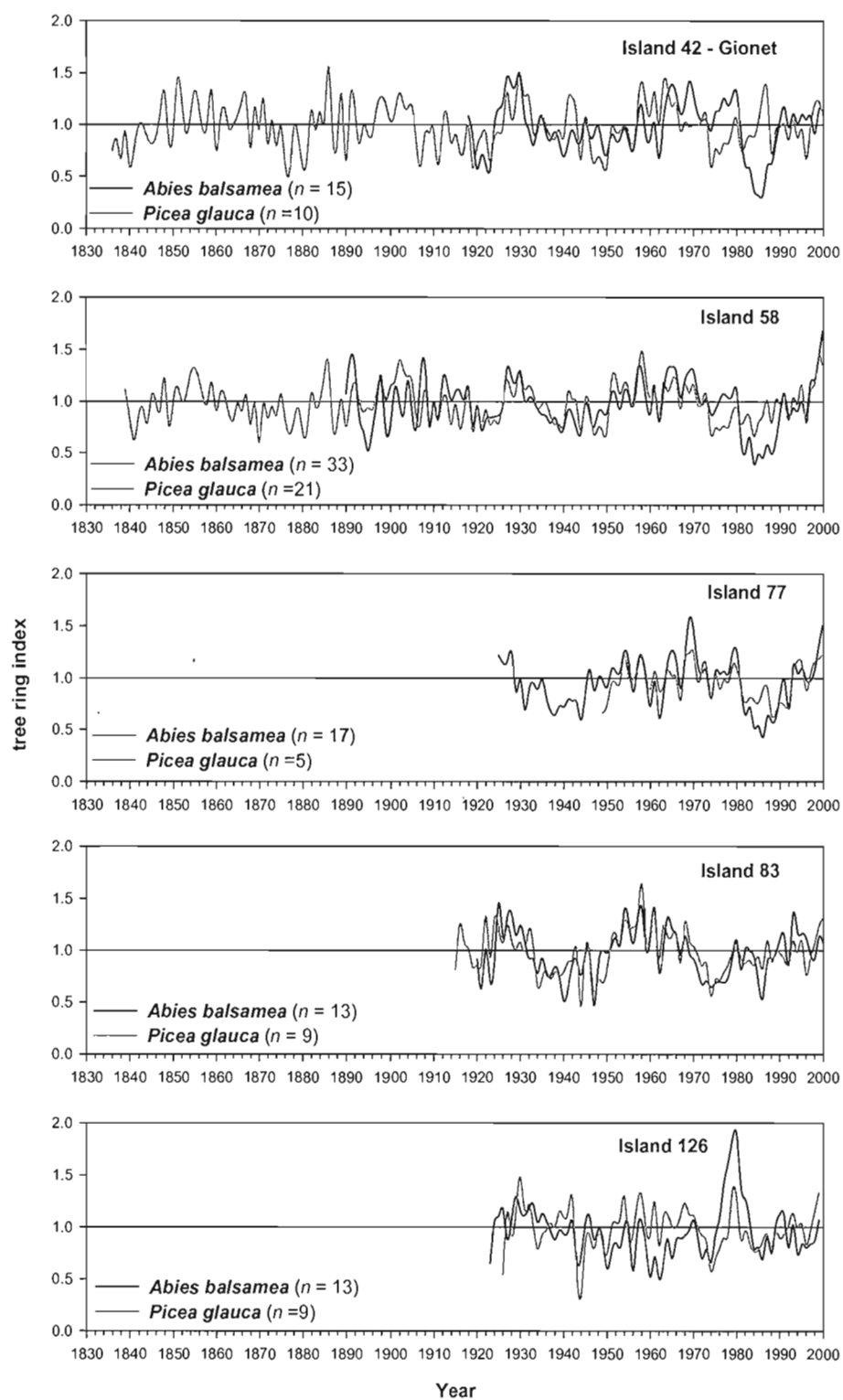
9.1 Frequency of budworm-caused defoliation in 216, 5 minute latitude by 5 min longitude cells, covering the Rouyn-Noranda region of northwest Québec (i.e., National topographic map 32D, 1:250 000 defoliation caused by spruce budworm. This measure provided an indication of both the extent and severity of budworm defoliation in our study region. Solid grey bars indicate the percentage of study area covered by any defoliated stands (light or severe) and black open bars indicate the percentage study area covered only by severe outbreaks.



9.2. Dendrochronological reconstruction of spruce budworm outbreaks on true islands in Lac Duparquet, northwestern Quebec.

9.2.1 Mean standardized chronologies of tree-ringwidth for hosts on true islands. Chronologies were developed following the methods presented in Chapter 3 and ringwidth data is presented only for years with greater than 3 data points (i.e., tree-ring series).





9.2.2 Timing and severity *Abies balsamea* growth reductions attributed to spruce budworm outbreaks on true islands. The program OUTBREAK was run on mean standardized tree-ring chronologies following methods in Chapter 2.

	Outbreak timing			Mean growth reduction (%)	Maximum growth reduction				Maximum rate of growth reduction	
	start	end	duration		year	departure [*]	index	reduction (%)	year	rate
Island 1	n/a	n/a	0	0	n/a		0	0	n/a	
Island 12	1905	1915	11	31.86	1907	-2.319	0.305	69.22	1905	2.58
	1981	1989	9	44.17	1982	-1.9	0.428	57.35	1981	1.79
Island 39	1877	1885	9	27.31	1880	-1.662	0.533	44.91	1877	2.37
	1905	1914	10	17.25	1911	-1.325	0.62	36.52	1914	1.65
	1970	1986	17	25.02	1984	-2.94	0.203	76.77	1986	2.86
Island 42	1917	1923	7	25.44	1923	-1.656	0.557	43.92	1920	1.28
	1981	1989	9	43.83	1985	-2.597	0.319	66.89	1981	1.54
Island 58	1848	1854	7	18.38	1849	-1.933	0.524	47.59	1849	2.14
	1981	1994	14	34.15	1984	-2.465	0.398	59.75	1981	2.03
Island 77	1904	1914	11	25.04	1910	-10.884	0.454	51.70	1914	1.77
	1931	1947	17	18.26	1944	-1.356	0.594	38.19	1929	1.43
	1981	1992	12	31.40	1986	-1.982	0.428	54.21	1981	1.31
Island 83	1918	1924	7	12.09	1921	-1.488	0.632	36.26	1919	3.1
	1932	1948	17	20.92	1947	-2.206	0.468	52.09	1947	2.21
	1970	1981	12	22.65	1974	-1.431	0.645	35.00	1981	1.26
	1984	1988	5	21.34	1986	-1.904	0.537	45.43	1985	1.07
Island 126	1947	1953	7	17.24	1950	-1.407	0.599	37.85	1950	1.1
	1959	1968	10	24.90	1962	-1.774	0.506	46.82	1960	1.09
Average			11	24.30		-1.900	0.486	50.00		1.71

* standard deviations from mean growth; mean growth =1 in master chronologies developed for each stand.

9.2.3 Timing and severity of *P. glauca* growth reductions attributed to spruce budworm on true islands. The program OUTBREAK was run on mean standardized tree-ring chronologies following methods in Chapter.

	Outbreak timing			Mean growth reduction (%)	Maximum growth reduction				Maximum rate of growth reductions	
	start	end	duration		year	departure *	index	reduction (%)	year	rate
<u>True islands:</u>										
Island01	1838	1845	8	22.52	1845	-2.377	0.515	45.38	1840	3.33
	1893	1899	7	7.22	1896	-1.507	0.685	28.03	1895	1.23
Island12	1974	1985	12	12.18	1974	-1.477	0.691	27.41	1974	1.86
	1872	1877	6	8.21	1876	-1.639	0.686	28.47	1876	1.99
	1934	1944	11	13.05	1944	-1.897	0.639	33.26	1944	1.04
	1981	1992	12	18.28	1985	-1.678	0.679	29.18	1981	2.19
Island39	1855	1860	6	11.26	1856	-1.534	0.672	28.46	1856	1.53
	1868	1872	5	0.84	1870	-1.447	0.689	26.72	1870	2.17
	1919	1926	8	16.29	1924	-1.878	0.605	35.29	1919	2.26
	1974	1989	16	11.25	1984	-1.97	0.587	37.13	1974	1.9
Island42	1828	1841	14	14.67	1835	-2.076	0.507	46.95	1828	4.09
	1874	1883	10	15.05	1877	-1.964	0.533	44.29	1868	2.13
	1906	1911	6	16.51	1907	-1.678	0.599	37.56	1906	1.57
	1914	1926	13	13.39	1919	-1.709	0.592	38.27	1919	1.76
	1944	1956	13	14.87	1950	-1.73	0.587	38.78	1944	1.95
	1974	1984	11	14.12	1974	-1.691	0.596	37.86	1974	2.09
	1992	1997	6	6.81	1996	-1.359	0.673	30.00	1988	2.56
Island58	1836	1847	12	7.42	1841	-1.871	0.624	34.57	1833	2.76
	1868	1881	14	12.66	1870	-2.012	0.597	37.33	1870	2.02
	1914	1925	12	12.51	1919	-1.433	0.708	26.00	1919	1.77
	1944	1950	7	17.39	1947	-1.564	0.683	28.55	1947	1.45
	1974	1988	15	15.83	1984	-1.679	0.661	30.80	1974	1.93
Island 77	1906	1916	11	16.03	1909	-1.796	0.425	53.10	1906	1.6
Island83	1934	1950	17	18.88	1944	-2.564	0.461	51.82	1944	2.62
	1971	1978	8	18.32	1974	-2.084	0.56	41.71	1974	1.49
Island 126	1943	1950	8	17.55	1944	-2.066	0.330	60.15	1943	2.41
Average			10.1	15.19		-1.787	0.578	38.94		1.90

* standard deviations from mean growth; mean growth =1 in master chronologies developed for each stand.

9.2.4 Characteristics of true islands sampled in Lac Duparquet.

	Island size (ha)	Distance to mainland (m)	Distance to nearest mainland host* forest (m)	Distance to nearest mainland <i>A.</i> <i>balsamea</i> - dominated forest
Island 01	0.34	107.38	552	552.00
Island 12	0.67	100.00	400.00	400.00
Island 39	78.71	1143.36	1129.36	2137.23
Island 42	37.23	1118.82	2416.26	3116.65
Island 58	5.75	61.80	263.25	1081.67
Island 77	1.34	880.39	804.56	1538.92
Island 83	1.86	400.00	527.20	1171.81
Island 126	8.39	265.32	691.30	691.30

* forests dominated by either *A. balsamea* or *P. glauca*.

9.2.5 Landscape composition surrounding of habitat islands (i.e., *A. balsamea*-dominated stands isolated in deciduous forest landscapes).

	Stand size (ha)	Composition of forest landscapes surrounding stands*					
		deciduous- dominated stands (%)		host- dominated forests (%)		<i>A. balsamea</i> dominated forests (%)	
		1000 m	500 m	1000 m	500 m	1000 m	500 m
Stand 2008N†	0.16	83	92	17	8	0	0
Stand 2006	0.06	80	74	20	26	10	14
Stand 2004	0.04	71	81	16	16	6	6
Stand 2010	4.00	75	54	25	1	25	1
Stand 9805N	1.50	63	34	32	21	16	0
Stand 9815N	0.22	63	37	33	1	13	0
Stand 9812	0.08	53	79	47	21	23	0
Stand 9910N	1.40	55	55	43	25	22	11

Note: stand numbers with an N beside them were plots established for the following study: Cappuccino, N., Lavertu, D., Bergeron, Y., and Régnière. 1998. Spruce budworm impact, abundance and parasitism rate in a patch landscape. *Oecologia*, 114: 236-242. They were revisited to take increment cores and assess budworm impacts on growth.

* forest composition within a 1000 m and 500 m radius of stand centroid.

† eight stands were selected from a larger sample of stands studied in northwestern Quebec (see Chapters 2 and 3). Stands were selected so that the oldest *A. balsamea* in stands were least 80 years of age, and the forested landscape within 1000m of the sample stands was comprised >50% deciduous-dominated forests.

9.2.6 Composition of host-dominated landscapes

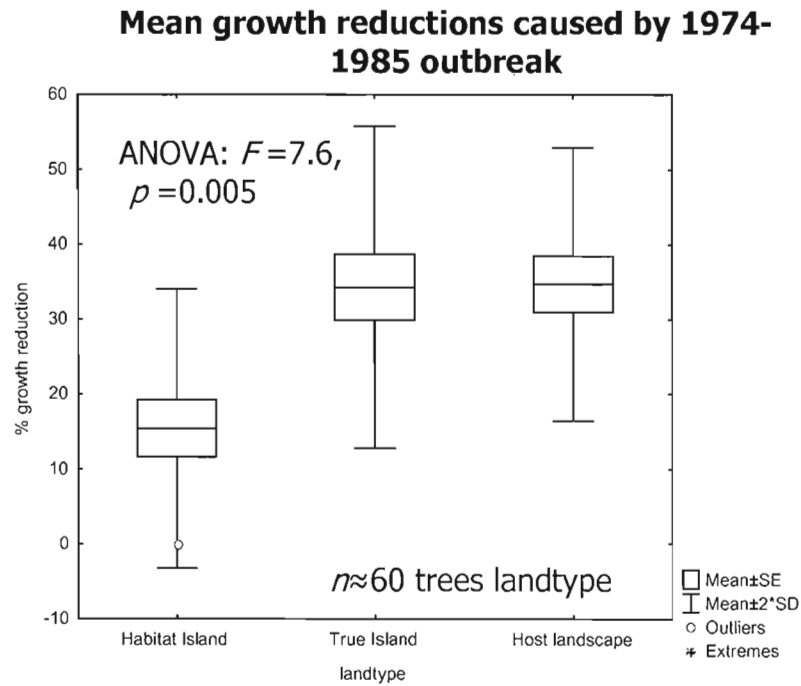
	Composition of forest landscapes surrounding stands*					
	<i>A. balsamea</i> dominated forests (%)		host-dominated forests (%)		Conifer† dominated forests (%)	
	1000 m	500 m	1000 m	500 m	1000 m	500 m
Stand 9803	77	61	95	88	97	88
Stand 9907	75	77	82	77	86	82
Stand 9813N	71	75	81	77	83	77
Stand 9806	75	54	80	74	84	74
Stand 9811N	64	91	73	91	76	96
Stand 9908N	58	87	75	84	77	84
Stand 9913	58	87	76	97	83	98
Stand 9903	55	55	90	55	91	99

Note: stand numbers with an N beside them were plots established for the following study: Cappuccino, N., Lavertu, D., Bergeron, Y., and Régnière. 1998. Spruce budworm impact, abundance and parasitism rate in a patch landscape. *Oecologia*, 114: 236-242. They were revisited to take increment cores and assess budworm impacts on growth.

* forest composition within a 1000 m and 500 m radius of stand centroid.

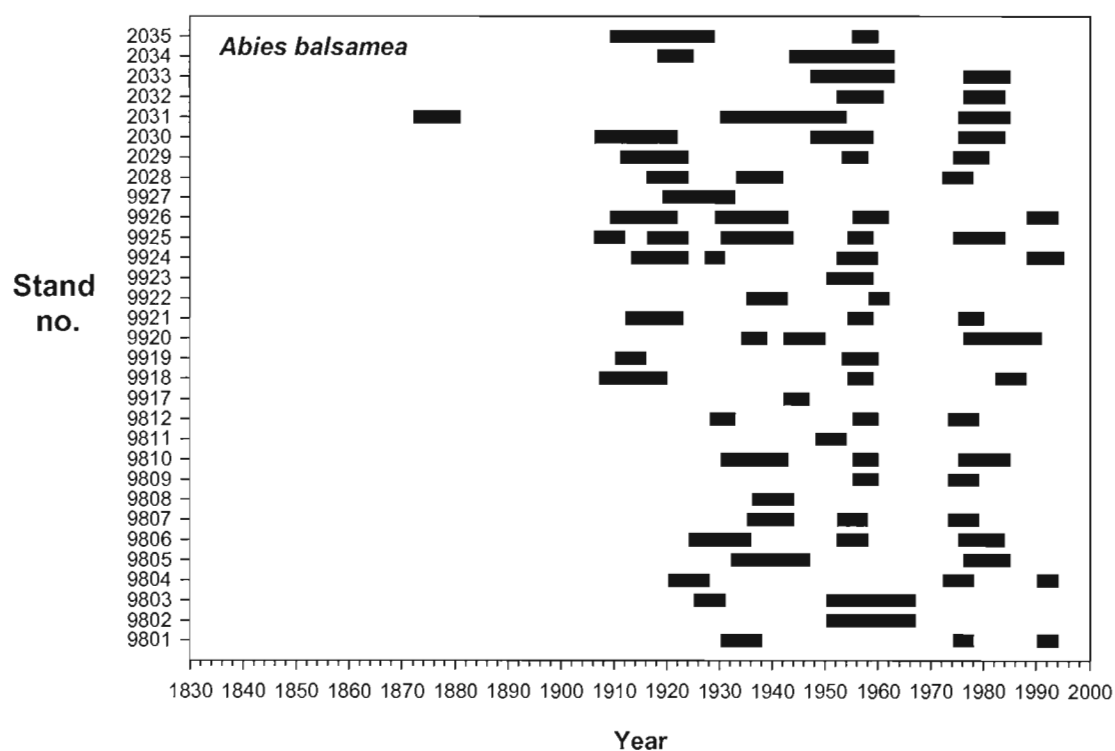
† includes conifer hosts (*A. balsamea* and *Picea glauca*, as well as non-host conifers *Pinus banksiana*, and *Thuja plicata*).

9.2.7 Box-plot illustrating the impacts of the last spruce budworm outbreak (1971-1985) on host growth on true islands, habitat islands and in *A. balsamea*-dominated landscapes. A Kruskal-Wallis one-way ANOVA (i.e., on ranked data) was used to test for significant differences among means.

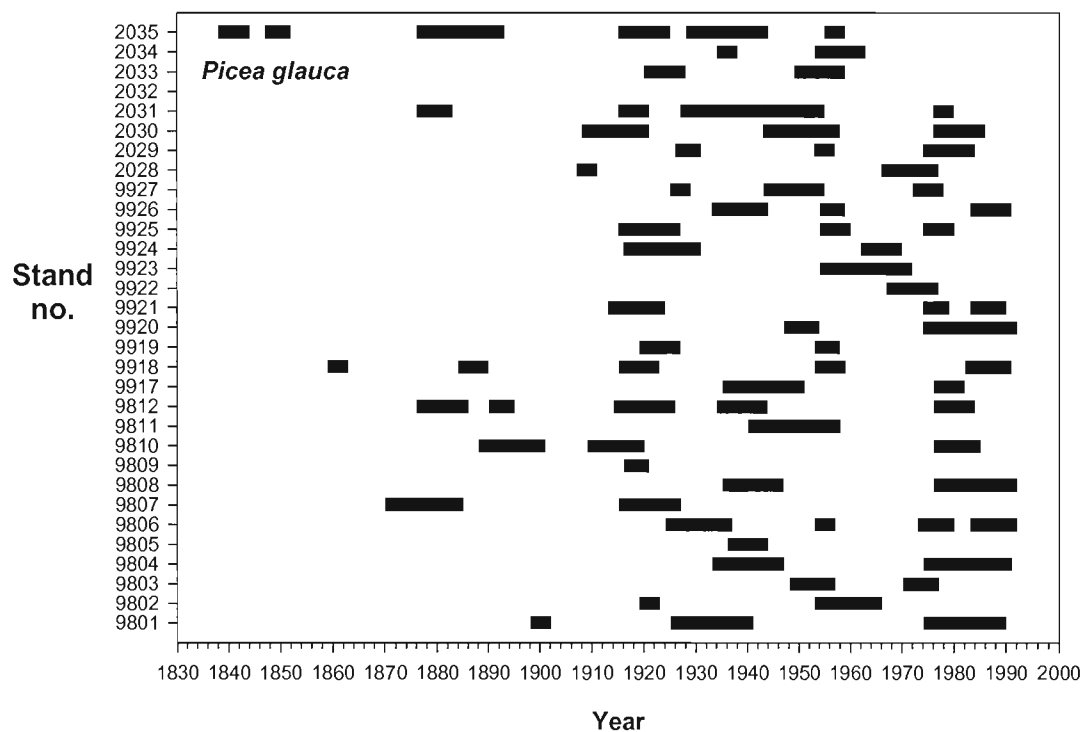


9.3. Dendrochronological reconstruction of budworm outbreaks over the last two centuries in northern New Brunswick.

9.3.1 Outbreaks inferred from growth reductions on *Abies balsamea*. See chapter 3 for dendrological methods.



9.3.2 Outbreaks inferred from growth reductions on *Picea glauca*. See chapter 3 for dendrological methods.



9.3.3 Timing and severity of *Abies balsamea* growth reductions attributed to spruce budworm outbreaks in northern New Brunswick.

Stand	Outbreak timing			Mean growth reduction (%)	Maximum growth reduction				Maximum rate of growth reduction	
	start	end	duration		year	departure *	index	reduction (%)	year	rate
9801	1930	1938	9	35.35	1933	-2.582	0.247	69.8	1933	1.77
	1974	1978	5	28.16	1976	-2.01	0.404	53.51	1974	1.79
	1990	1994	5	9.6	1990	-1.434	0.562	37.12	1990	1.64
9802	1950	1967	18	20.08	1958	-1.581	0.527	42.76	1953	1
9803	1925	1931	7	20.21	1928	-1.421	0.35	58.38	1914	3.53
	1950	1967	18	33.57	1954	-1.407	0.356	57.76	1950	0.66
9804	1920	1928	9	7.65	1924	-1.448	0.758	19.69	1921	0.78
	1972	1978	7	19.73	1976	-3.468	0.443	52.36	1976	1.34
	1990	1994	5	11.6	1992	-1.551	0.742	21.35	1992	0.84
9805	1932	1947	16	19.51	1944	-1.948	0.5	44.54	1932	2.45
	1976	1985	10	14.41	1977	-2.136	0.455	49.21	1977	1.46
9806	1924	1936	13	10.24	1925	-2.987	0.394	56.23	1925	1.62
	1952	1958	7	24.98	1954	-2.346	0.518	43.37	1954	1.67
	1975	1984	10	9.3	1976	-2.103	0.565	38.49	1976	1.51
9807	1935	1944	10	34.2	1940	-1.919	0.418	51.28	1935	2.04
	1952	1958	7	8.92	1956	-1.68	0.484	44.43	1955	1.13
	1973	1979	7	18.09	1976	-1.441	0.55	37.59	1976	1.22
9808	1936	1944	9	22.34	1940	-1.618	0.596	34.11	1936	2.38
9809	1955	1960	6	10.72	1956	-1.888	0.638	32.5	1955	1.15
	1973	1979	7	22.13	1977	-2.223	0.576	38.94	1976	1.38
9810	1930	1943	14	12.79	1938	-1.384	0.673	28.32	1930	0.7
	1955	1960	6	21.33	1956	-1.926	0.552	40.87	1956	1.49
	1975	1985	11	21.2	1977	-2.119	0.509	45.33	1976	1.45
9811	1948	1954	7	35.12	1950	-2.827	0.239	68.61	1948	2.54
9812	1928	1933	6	19.15	1928	-1.551	0.594	36.97	1928	1.91
	1955	1960	6	14.85	1956	-1.488	0.61	35.31	1955	1.69
	1973	1979	7	18.08	1978	-1.472	0.614	34.89	1973	1.47
9917	1942	1947	6	35.64	1945	-2.57	0.403	51.89	1945	0.95
9918	1907	1920	14	14.68	1915	-2.613	0.46	49.85	1920	3.44
	1954	1959	6	14.47	1957	-1.546	0.671	27.96	1954	0.95
	1982	1988	7	15.26	1984	-2.567	0.469	48.91	1988	1.27
9919	1910	1916	7	38.26	1915	-2.691	0.197	74.23	1914	2.47
	1953	1960	8	32.02	1958	-2.305	0.305	63.03	1954	1.25
	1934	1939	6	21.66	1935	-2.125	0.52	40.99	1934	2.18
	1942	1950	9	10.69	1942	-1.475	0.652	27.3	1942	1.58
	1976	1991	16	13.56	1978	-1.982	0.549	37.98	1977	1.53

9.3.3 (cont.)

Stand	Outbreak timing				Mean growth reduction (%)	Maximum growth reduction				Maximum rate of growth reduction	
	start	end	duration	year		departure *	index	reduction (%)	year	rate	
9920	1934	1939	6	23.97	1935	-2.125	0.52	42.37	1934	1.94	
	1942	1950	9	13	1942	-1.475	0.652	28.99	1942	1.58	
	1976	1991	16	15.87	1978	-1.982	0.549	39.43	1977	1.53	
9921	1912	1923	12	25.01	1915	-2.486	0.427	53.57	1912	2.94	
	1954	1959	6	9.44	1954	-1.752	0.59	36.66	1954	2.08	
	1975	1980	6	24.99	1977	-2.674	0.385	57.92	1976	1.55	
9922	1935	1943	9	11.66	1938	-1.693	0.605	32.78	1936	1.36	
	1958	1962	5	11.38	1959	-1.65	0.614	31.84	1958	1.29	
9923	1950	1959	10	16.9	1954	-2.383	0.424	53.13	1954	1.95	
9924	1913	1924	12	13.23	1923	-2.098	0.441	51.62	1919	2.05	
	1927	1931	5	29.68	1928	-2.322	0.384	57.53	1928	1.57	
	1952	1960	9	8.86	1954	-1.402	0.618	33.26	1952	1.51	
	1988	1995	8	11.95	1990	-1.481	0.598	35.33	1994	1.48	
9925	1906	1912	7	12.34	1909	-1.325	0.651	29.08	1906	1.11	
	1916	1924	9	12.81	1917	-1.371	0.64	30.22	1916	1.29	
	1930	1944	15	12.05	1938	-1.4	0.633	30.94	1927	0.73	
	1954	1959	6	28.26	1957	-2.242	0.432	51.8	1954	1.67	
	1974	1984	11	13.28	1977	-2.116	0.462	48.68	1976	1.41	
9926	1909	1922	14	11.76	1915	-2.36	0.278	69.39	1909	4.14	
	1929	1943	15	17.49	1938	-1.59	0.508	45.53	1938	0.52	
	1955	1962	8	19.96	1958	-2.022	0.379	58.91	1956	1.07	
	1988	1994	7	17.29	1990	-1.312	0.591	36.92	1988	1.17	
9927	1919	1933	15	32.26	1930	-2.069	0.34	61	1919	2.63	
2028	1916	1924	9	19.19	1920	-2.713	0.352	58.76	1919	2.98	
	1933	1942	10	21.16	1938	-1.623	0.594	33.65	1933	1.24	
	1972	1978	7	22.41	1976	-2.307	0.442	49.42	1972	1.55	
2029	1911	1924	14	27.94	1916	-3.154	0.168	75.85	1919	1.82	
	1953	1958	6	16.33	1956	-1.793	0.499	41.51	1956	1.53	
	1974	1981	8	20.84	1976	-1.727	0.515	39.85	1975	1.32	
2030	1906	1922	17	32.99	1916	-2.36	0.222	70.59	1922	0.88	
	1947	1959	13	25.76	1954	-1.958	0.344	57.94	1958	0.75	
	1975	1984	10	13.84	1976	-1.401	0.513	40.41	1976	1.22	
2031	1872	1881	10	48.82	1877	-2.428	0.18	76.17	1872	2.82	
	1930	1954	25	18.09	1953	-1.501	0.474	45.67	1953	1.03	
	1975	1985	11	31.82	1977	-2.17	0.262	67.66	1976	1.35	
2032	1952	1961	10	46.56	1958	-2.707	0.085	88.98	1956	0.66	
	1976	1984	9	25.55	1977	-1.544	0.469	49.14	1977	1.49	
2033	1947	1963	17	23.9	1954	-2.14	0.347	61.62	1950	0.73	
	1976	1985	10	21.42	1977	-1.828	0.439	52.07	1977	1.57	
2034	1918	1925	8	-2.98	1920	-1.325	0.651	30.15	1920	3.93	
	1943	1963	21	12.11	1958	-1.808	0.532	42.49	1950	0.96	
2035	1909	1929	21	30.71	1921	-2.376	0.267	65.29	1909	0.87	
	1955	1960	6	23.26	1958	-1.773	0.436	47.76	1956	1.08	
Average			9.91139	20.16		-1.973	0.476	46.93		1.6023	

9.3.4 Timing and severity (%) of *Picea glauca* growth reductions attributed to spruce defoliation budworm outbreaks.

Stand	Outbreak timing			Mean growth reduction (%)	Maximum growth reduction				Maximum rate of growth reduction	
	start	end	duration		year	departure *	index	reduction (%)	year	rate
9801	1898	1902	5	-9.85	1898	-1.849	0.399	56.62	1900	4.38
	1925	1941	17	24.19	1936	-1.916	0.378	58.78	1928	0.81
	1974	1990	17	22.27	1984	-1.919	0.377	58.88	1974	1.4
9802	1919	1923	5	12.07	1922	-1.473	0.561	40.86	1921	1.01
	1953	1966	14	30.35	1957	-2.304	0.321	65.56	1953	1.05
9803	1948	1957	10	30.19	1954	-2.395	0.341	63.24	1948	2.22
9804	1933	1947	15	12.69	1935	-1.953	0.599	37.04	1933	2.95
	1970	1977	8	16.21	1976	-2.286	0.533	43.83	1974	1.64
9805	1936	1944	9	33.61	1942	-2.26	0.436	51.75	1936	1.28
	1974	1991	18	9.81	1977	-1.604	0.59	35.90	1977	1.28
9806	1924	1937	14	5.51	1926	-1.395	0.71	24.61	1926	1.59
	1953	1957	5	22.72	1954	-1.901	0.613	34.59	1953	1.49
	1973	1980	8	15.08	1976	-2.7	0.46	50.33	1973	1.18
	1983	1992	10	10.57	1985	-1.306	0.727	22.86	1983	1.82
9807	1870	1885	16	39.59	1878	-2.101	0.26	71.50	1870	1.57
	1915	1927	13	33.01	1917	-2.247	0.21	76.64	1915	2.22
9808	1935	1947	13	13.81	1942	-1.96	0.555	41.11	1942	1.68
	1976	1991	16	15.11	1977	-2.336	0.473	49.55	1976	2.11
9809	1916	1921	6	20.88	1917	-2.038	0.524	43.23	1917	1.4
	1928	1936	9	14.96	1932	-1.619	0.616	33.77	1934	1.32
	1973	1979	7	20.85	1977	-2.106	0.509	44.78	1976	1.36
	1988	1992	5	15.72	1989	-1.938	0.546	40.97	1988	1.6
9810	1888	1901	14	29.10	1898	-1.601	0.515	44.88	1888	1.45
	1909	1920	12	22.09	1915	-1.915	0.424	54.24	1915	1.51
	1976	1985	10	12.60	1977	-1.525	0.537	42.61	1976	1.4
9811	1940	1958	19	20.93	1947	-2.008	0.418	53.83	1940	1.76
9812	1876	1886	11	19.11	1883	-1.72	0.516	43.88	1882	1.06
	1890	1895	6	16.13	1893	-2.193	0.391	56.74	1890	2.05
	1914	1926	13	21.37	1918	-2.076	0.422	53.55	1914	1.65
	1934	1944	11	13.68	1940	-1.414	0.597	35.54	1940	0.58
	1976	1984	9	22.37	1977	-1.758	0.506	44.91	1976	1.99
9917	1935	1951	17	15.73	1939	-2.268	0.54	40.36	1939	1.51
	1976	1982	7	9.23	1977	-2.365	0.522	42.21	1977	1.89
9918	1859	1863	5	7.07	1863	-1.323	0.687	27.44	1863	1.31
	1884	1890	7	11.59	1887	-1.529	0.641	32.17	1876	1.78
	1915	1923	9	27.71	1917	-3.212	0.266	70.76	1915	1.59
	1953	1959	7	34.14	1957	-2.525	0.419	55.02	1954	1.57
	1982	1991	10	20.36	1984	-1.933	0.551	41.43	1982	1.2
9919	1919	1927	9	11.30	1920	-2.437	0.552	40.62	1923	0.56
	1953	1958	6	21.12	1954	-2.587	0.526	43.29	1954	1.93
9920	1947	1954	8	21.71	1950	-1.66	0.473	48.63	1947	2.56

Table 9.3.4 (cont.)

Stand	Outbreak timing			Mean growth reduction (%)	Maximum growth reduction				Maximum rate of growth reduction	
	start	end	duration		year	departure *	index	reduction (%)	year	rate
9921	1974	1992	19	24.72	1989	-2.035	0.36	60.26	1976	1.08
	1913	1924	12	26.86	1915	-2.312	0.373	58.38	1915	2.66
	1974	1979	6	23.84	1977	-2.385	0.354	60.34	1976	1.2
	1983	1990	8	11.79	1984	-1.792	0.507	44.59	1984	1.53
9922	1967	1977	11	25.15	1976	-1.985	0.331	59.49	1976	1.22
9923	1954	1972	19	37.26	1970	-2.064	0.365	56.55	1952	1.69
9924	1916	1931	16	20.83	1919	-2.644	0.414	53.39	1929	2.31
	1962	1970	9	11.60	1967	-1.494	0.652	28.90	1962	1.97
9925	1915	1927	13	29.08	1917	-2.821	0.242	71.61	1915	3.18
	1954	1960	7	23.70	1957	-1.886	0.482	46.91	1954	1.6
	1974	1980	7	18.03	1976	-1.933	0.47	48.14	1974	1.45
9926	1933	1944	12	29.69	1940	-2.334	0.352	62.99	1938	0.87
	1954	1959	6	18.53	1957	-1.368	0.617	35.72	1954	1.51
	1983	1991	9	12.07	1984	-1.31	0.633	34.08	1984	1.16
9927	1925	1929	5	12.46	1927	-1.319	0.734	23.79	1925	1.44
	1943	1955	13	9.64	1954	-1.711	0.657	31.72	1954	1.55
	1972	1978	7	16.39	1977	-3.145	0.375	60.73	1976	2.16
2028	1907	1911	5	29.36	1907	-3.054	0.315	63.18	1907	2.91
	1966	1977	12	20.77	1976	-2.45	0.442	50.11	1966	1.45
2029	1926	1931	6	11.64	1927	-1.699	0.586	36.25	1926	2.29
	1953	1957	5	24.57	1954	-1.971	0.525	42.52	1953	1.73
	1974	1984	11	17.45	1976	-2.694	0.363	59.19	1976	1.37
2030	1908	1921	14	26.95	1915	-2.641	0.161	77.37	1919	3.18
	1943	1958	16	13.52	1954	-1.771	0.418	50.93	1954	0.72
	1976	1986	11	20.44	1984	-1.987	0.354	57.51	1976	1.28
2031	1876	1883	8	52.75	1880	-2.035	0.26	67.36	1876	2.71
	1915	1921	7	45.28	1917	-2.312	0.167	76.93	1915	2.25
	1927	1955	29	21.82	1940	-1.388	0.477	45.04	1952	0.99
2032 No spruce sampled				0.00				0.00		
	1976	1980	5	25.53	1977	-1.564	0.418	51.11	1976	1.17
2033	1920	1928	9	22.92	1922	-2.707	0.105	78.45	1921	5.61
	1949	1959	11	17.42	1954	-2.303	0.223	66.31	1953	1.54
2034	1934	1938	5	9.15	1934	-1.673	0.652	31.93	1934	4.78
	1953	1963	11	15.93	1958	-2.02	0.582	39.13	1953	1.53
2035	1838	1844	7	26.77	1843	-3.095	0.197	76.65	1835	2.5
	1847	1852	6	10.27	1849	-1.494	0.597	35.49	1847	1.58
	1876	1893	18	9.70	1890	-1.594	0.572	38.06	1879	1.36
	1915	1925	11	25.20	1917	-2.507	0.344	61.52	1916	1.59
	1928	1944	17	12.47	1943	-1.794	0.522	43.20	1943	1.31
	1955	1959	5	22.05	1957	-1.742	0.535	41.87	1956	1.48
Average				19.76		-2.03	0.460	48.72		1.76

9.4.

9.4.1. Annual climate variables generated for each stand sampled in New Brunswick using BioSIM (Régnière 1996). Instrumental weather data for each stand interpolated from the 4 nearest stations over the period 1970-1998.

Stand	Ecoregion	Elev (m)	MAT	MST	FFP	DD>0	DD>5	DD>10	MAP	MSP	AI [†]	WVPD	TotRad	PET
1	Northern Uplands	361	2.7	13.2	110.1	2320.3	1356.5	633.5	1054.3	488.8	3.8	1264.2	3819.7	40.3
2	Central Highlands	505	2.1	12.5	102.6	2173.6	1242.2	554.0	1013.3	493.6	3.4	1136.9	3691.8	38.8
3	Northern Uplands	350	2.5	13.0	111.1	2279.6	1323.7	607.9	1073.5	497.5	3.4	1267.3	3810.8	39.9
4	Northern Uplands	243	3.2	13.8	113.8	2443.2	1453.4	698.0	1139.3	504.6	3.8	1437.7	4000.1	41.6
5	Northern Uplands	378	1.7	12.7	88.2	2209.5	1267.3	562.7	1014.7	498.6	2.3	1380.0	4073.0	39.2
6	Northern Uplands	265	3.1	13.7	111.5	2426.2	1440.4	689.8	1127.5	501.3	3.8	1416.3	3981.8	41.4
7	Northern Uplands	287	2.1	13.0	98.4	2276.2	1320.4	602.2	1017.4	495.4	2.3	1385.4	4014.6	39.9
8	Central Highlands	367	1.9	12.8	84.7	2233.6	1284.0	573.1	1022.0	501.4	2.2	1412.9	4128.3	39.5
9	Northern Uplands	288	2.1	13.0	103.7	2281.3	1326.2	607.5	1027.8	498.0	2.3	1347.4	3931.9	39.9
10	Northern Uplands	300	2.0	12.9	97.1	2262.8	1310.3	594.8	1010.7	494.8	2.3	1382.1	4020.7	39.7
11	Central Highlands	283	2.6	13.3	93.6	2360.8	1377.5	636.0	1078.9	505.6	2.7	1477.7	4180.1	40.8
12	Northern Uplands	249	2.2	13.1	101.2	2308.0	1345.0	619.3	1014.1	491.2	2.4	1407.5	4033.5	40.2
13	Northern Uplands	389	1.7	12.6	85.6	2199.5	1259.8	557.6	1014.6	499.4	2.2	1373.4	4066.6	39.1
14	Northern Uplands	210	3.0	13.5	115.0	2401.4	1415.7	675.4	1035.9	484.0	3.4	1325.9	3832.9	41.1
15	Northern Uplands	247	2.9	13.4	114.9	2369.6	1391.1	657.6	1035.4	486.7	3.4	1307.4	3824.5	40.8

Table 9.4.1 (cont.)

16	Northern Uplands	378	1.7	12.7	88.2	2209.5	1267.3	562.7	1014.7	498.6	2.3	1380.0	4073.0	39.2
17	Northern Uplands	549	1.8	12.3	92.7	2140.5	1212.4	528.3	1040.3	512.0	2.8	1217.9	3868.9	38.5
18	Northern Uplands	247	2.7	13.3	117.7	2330.8	1363.2	638.5	1061.7	511.3	2.6	1260.8	3708.4	40.4
19	Northern Uplands	344	2.3	13.0	114.4	2263.1	1314.3	604.4	1072.4	515.8	2.4	1226.1	3696.3	39.6
20	Northern Uplands	326	2.4	13.1	114.4	2282.1	1328.7	614.4	1073.4	514.3	2.5	1242.9	3717.3	39.8
21	Northern Uplands	177	3.1	13.6	120.7	2395.5	1412.5	672.8	1038.8	466.3	3.8	1278.7	3741.7	41.1
22	Highlands	443	1.6	12.4	81.9	2144.8	1215.3	528.4	1097.6	536.6	1.4	1292.9	3908.5	38.7
23	Northern Uplands	191	3.0	13.6	118.4	2405.7	1423.1	680.9	1071.9	502.1	2.8	1330.9	3804.0	41.2
24	Northern Uplands	198	3.4	14.0	117.1	2495.0	1494.6	728.5	1136.3	496.8	4.1	1459.0	4006.8	42.1
25	Northern Uplands	302	2.8	13.3	114.7	2347.1	1376.9	645.6	1084.6	496.0	3.5	1302.4	3826.0	40.6
26	Highlands	400	2.6	13.1	106.8	2298.7	1335.4	617.4	1033.1	491.0	3.5	1246.5	3832.3	40.1
27	Northern Uplands	511	1.9	12.5	93.0	2175.1	1238.4	545.9	1042.9	508.5	2.9	1241.6	3893.7	38.8
28	Highlands	384	2.8	13.3	106.1	2351.3	1374.7	644.6	1125.9	520.7	3.1	1343.0	3963.6	40.6
29	Northern Uplands	462	2.0	12.5	111.9	2162.8	1236.7	551.5	1023.2	500.1	2.9	1135.8	3628.3	38.6
30	Northern Uplands	430	2.1	12.7	92.5	2228.8	1276.9	568.9	1055.8	504.8	2.7	1340.8	4018.5	39.4
31	Northern Uplands	327	2.0	12.9	105.6	2256.7	1309.5	596.4	1027.2	501.9	2.4	1285.4	3834.9	39.6

Table 9.4.1 (cont.)

Average	335.1	2.4	13.1	104.1	2291.4	1332.0	612.9	1054.2	500.6	2.9	1319.6	3901.1	40.0
Minimum	177	1.6	12.3	81.9	2140.5	1212.4	528.3	1010.7	466.3	1.4	1135.8	3628.3	38.5
Maximum	549	3.4	14.0	120.7	2495.0	1494.6	728.5	1139.3	536.6	4.1	1477.7	4180.1	42.1

* MAT = mean annual temperature (°C); MST mean summer temperature (°C); NFFD=Number of frost-free days-number of days >0 °C in a year;
 FFP=Frost-free period – number consecutive days >0 °C; DD>0=degree days >0 °C; DD>5=degree days >5 °C; DD>10=degree days >10 °C;
 MAP=Mean annual precipitation (mm); MSP=mean summer precipitation; aridity index= potential evapotranspiration-total annual precipitation (mm water); WVPD=water vapour pressure deficit (mBar); TotRad=Total radiation (megajoules/m²/year); PET= Potential evaporation (mm water).

† AI = Aridity index .

9.4.2. Selected seasonal climate variables (i.e., those thought to impact budworm populations and host vulnerability) generated for each stand using BioSIM (Régnière 1996). Instrumental weather data for each stand interpolated from the 4 nearest stations over the period 1970-1998.

stand#	Ecoregion	Elev*	MINTW	MAXTW	MINTSP	MINTSU	MAXTSU
1	Northern Uplands	361	-16.1	-6.2	-4.1	8.1	19.4
2	Central Highlands	505	-16.4	-6.8	-4.5	7.8	18.4
3	Northern Uplands	350	-16.1	-6.4	-4.2	8.0	19.3
4	Northern Uplands	243	-16.2	-5.4	-3.9	5.4	17.6
5	Northern Uplands	378	-18.5	-7.4	-5.0	7.0	20.0
6	Northern Uplands	265	-16.4	-5.5	-4.1	8.1	20.5
7	Northern Uplands	287	-18.3	-7.4	-4.7	7.4	20.2
8	Central Highlands	367	-18.6	-7.2	-4.9	7.0	20.2
9	Northern Uplands	288	-18.1	-7.5	-4.6	7.5	20.0
10	Northern Uplands	300	-18.3	-7.5	-4.7	7.3	20.1
11	Central Highlands	283	-18.4	-5.9	-4.8	7.3	20.7
12	Northern Uplands	249	-18.2	-7.2	-4.6	7.4	20.4
13	Northern Uplands	389	-18.5	-7.5	-5.0	7.0	19.9
14	Northern Uplands	210	-16.3	-6.1	-3.7	8.5	20.0
15	Northern Uplands	247	-16.5	-6.1	-3.9	8.3	20.0
16	Northern Uplands	378	-18.5	-7.4	-5.0	7.0	20.0
17	Northern Uplands	549	-17.4	-7.0	-5.0	7.2	18.7
18	Northern Uplands	247	-16.6	-6.8	-4.0	8.2	19.7
19	Northern Uplands	344	-16.9	-7.1	-4.3	7.9	19.4
20	Northern Uplands	326	-16.9	-7.0	-4.3	7.8	19.3
21	Northern Uplands	177	-15.4	-5.8	-3.5	8.6	19.8
22	Northern Uplands	443	-18.7	-8.0	-5.1	6.9	19.5
23	Northern Uplands	191	-16.5	-6.5	-3.7	8.7	20.2
24	Northern Uplands	198	-15.9	-5.2	-3.7	8.4	20.8
25	Northern Uplands	302	-16.1	-6.0	-4.1	8.1	19.8
26	Highlands	400	-16.4	-6.2	-4.1	8.1	19.4
27	Northern Uplands	511	-17.4	-6.8	-4.9	7.3	18.9
28	Highlands	384	-16.8	-5.5	-4.5	7.5	20.3
29	Northern Uplands	462	-16.8	-7.3	-4.7	7.6	18.4
30	Northern Uplands	430	-17.8	-6.7	-4.9	7.2	19.6
31	Northern Uplands	327	-18.0	-7.7	-4.6	7.6	19.7
Average		335.2	-17.2	-6.7	-4.4	7.6	19.7
Minimum		177.0	-18.7	-8.0	-5.1	5.4	17.6
Maximum		549.0	-15.4	-5.2	-3.5	8.7	20.8

* Elev=Elevation (m); MINTW = minimum winter temperature (°C); MAXTW = maximum winter temperature; MINTSP=Minimum spring temperature; MINTSU = minimum summer temperature; MAXSU = maximum summer temperature.

9.4.3 Selected monthly climate variables (i.e., those thought to impact budworm populations and host vulnerability) generated for each stand using BioSIM (Régnière 1996). Instrumental weather data for each stand interpolated from the 4 nearest stations over the period 1970-1998.

stand		Elev	MINT5	MINT6	MINT7	MINT8	MAXT5	MAXT6	MAXT7	MAXT8	PPTS	PPT5	PPT6	PPT7	PPT8
#	Ecoregion														
1	Northern Uplands	361	2.3	8.0	11.6	10.6	13.8	19.8	22.7	21.4	103.5	97.5	96.8	112.2	107.5
2	Central Highlands	505	2.0	7.7	11.1	10.2	12.9	18.9	21.7	20.3	103.5	94.6	98.7	116.2	107.1
3	Northern Uplands	350	2.2	7.9	11.4	10.5	13.6	19.6	22.6	21.4	104.2	97.6	97.5	113.0	108.5
4	Northern Uplands	243	-0.2	3.0	8.9	9.9	12.1	15.3	20.9	21.8	105.4	93.2	98.6	117.2	112.5
5	Northern Uplands	378	1.8	7.2	10.3	8.8	14.7	20.5	23.0	21.7	103.2	87.1	95.5	123.3	106.7
6	Northern Uplands	265	2.3	8.0	11.6	10.6	15.0	20.8	23.8	22.6	104.9	101.3	97.8	113.3	107.1
7	Northern Uplands	287	2.0	7.6	10.7	9.2	14.9	20.7	23.2	22.1	102.9	87.7	94.8	122.7	106.4
8	Central Highlands	367	1.8	7.1	10.2	8.7	15.0	20.7	23.2	21.9	102.8	88.4	95.3	121.4	104.5
9	Northern Uplands	288	2.1	7.7	10.9	9.5	14.7	20.5	23.0	21.9	101.9	87.3	93.2	120.8	106.2
10	Northern Uplands	300	2.0	7.5	10.7	9.2	14.8	20.7	23.1	22.0	102.5	86.1	94.3	123.1	106.5
11	Central Highlands	283	2.0	7.4	10.5	9.1	15.6	21.2	23.7	22.3	104.4	92.1	96.6	117.3	111.4
12	Northern Uplands	249	2.1	7.6	10.8	9.3	15.1	20.9	23.4	22.3	102.2	87.0	94.2	122.0	105.8
13	Northern Uplands	389	1.7	7.1	10.3	8.7	14.7	20.4	23.0	21.7	103.4	87.1	95.7	123.6	107.0
14	Northern Uplands	210	2.7	8.5	10.9	10.9	14.4	20.5	21.9	21.9	99.4	90.4	94.3	103.7	103.7

Table 9.4.3 (cont.)

15	Northern Uplands	247	2.6	8.3	11.7	10.7	14.4	20.5	23.3	21.7	102.3	92.2	98.3	112.3	106.5
16	Northern Uplands	378	1.8	7.2	10.3	8.8	14.7	20.5	23.0	21.7	103.2	87.1	95.5	123.3	106.7
17	Northern Uplands	549	1.7	7.2	10.6	9.4	13.4	19.2	21.9	20.4	104.5	93.6	100.1	116.5	107.7
18	Northern Uplands	247	2.4	8.2	11.6	10.6	14.2	20.1	23.0	21.6	101.8	94.5	95.9	110.6	106.0
19	Northern Uplands	344	2.1	7.9	11.4	10.3	13.9	19.8	22.6	21.2	103.2	95.9	97.6	112.8	106.4
20	Northern Uplands	326	2.2	7.9	11.4	10.3	14.0	19.9	22.8	21.3	103.3	95.7	97.6	112.7	106.3
21	Northern Uplands	177	2.6	8.5	12.1	11.3	13.9	20.1	23.2	22.1	97.7	94.6	91.3	106.6	98.3
22	Northern Uplands	443	1.7	7.1	10.0	8.8	14.5	19.8	22.4	21.2	107.8	96.7	96.0	129.7	108.7
23	Northern Uplands	191	2.8	8.7	12.2	11.0	14.6	20.6	23.5	22.1	98.4	91.1	93.6	106.4	102.7
24	Northern Uplands	198	2.6	8.2	11.9	10.9	15.1	21.0	24.1	23.0	103.1	100.8	95.3	111.1	105.1
25	Northern Uplands	302	2.3	7.9	11.5	10.7	14.1	20.1	23.1	21.9	105.0	100.0	97.8	114.9	107.2
26	Northern Highlands	400	2.5	8.0	11.4	10.3	13.9	19.8	22.6	21.2	101.4	92.7	97.2	111.5	104.3
27	Northern Uplands	511	1.8	7.3	10.7	9.5	13.6	19.4	22.1	20.7	103.7	93.1	99.1	115.3	107.1
28	Northern Highlands	384	1.8	7.6	11.0	9.8	15.0	20.7	23.5	22.1	109.7	111.6	111.8	114.0	101.3
29	Northern Uplands	462	1.7	7.5	11.1	10.1	12.8	18.8	21.7	20.3	102.0	94.8	97.4	111.5	104.5
30	Northern Uplands	430	1.8	7.2	10.5	9.3	14.3	20.1	22.7	21.2	103.0	92.7	96.6	114.8	108.0
31	Northern Uplands	327	2.0	7.8	11.0	9.7	14.2	20.1	22.7	21.5	103.7	89.2	95.7	120.0	109.3
	Average	335.2	2.0	7.6	11.0	9.9	14.3	20.0	22.8	21.6	103.2	93.3	96.8	115.9	106.4

Elev=elevation (m); MIN and MAXT5,6,7,8 = minimum and maximum temperatures (°C) in May, June, July, and August, respectively; PPTS=total summer precipitation (mm). PPT5,6,7,8=total precipitation in May, June, July and August, respectively.

9.5. Summary of partial regression analyses used to partition variation in budworm-caused growth reductions in 31 balsam fir-spruce stands sampled in New Brunswick among purely spatial (i.e., latitude and longitude), purely environmental (i.e., the explanatory variables of interest –Hw= Surrounding forest hardwood content, EL=elevation, SP=presence of spraying for individual years and cumulative number of years sprayed for periods of time), joint spatial-environmental and unexplained variation.

